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..... PAT HUTCHINGS & CHRIS GLASBY

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The Amphitritinae (Polychaeta: Terebellidae) from Australia

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ABSTRACT. The amphitritine fauna of Australia comprises 17 genera and 37 species. These are described, and a key to the genera and Australian species is provided. Twenty one new species and one new genus are described: *Amphitrite pachyderma* n. sp., *Amphitritides harpa* n. sp., *A. ithya* n. sp., *Arranooba booromia* n. gen., n. sp., *Baffinia biseriata* n. sp., *Eupolymnia koorangia* n. sp., *Lanassa exelysis* n. sp., *L. ocellata* n. sp., *Lanicides fascia* n. sp., *L. lacuna* n. sp., *L. tribranchiata* n. sp., *Lanice bidewa* n. sp., *Loimia batilla* n. sp., *L. triloba* n. sp., *Neoleprea macrocercus* n. sp., *Phisidia echuca* n. sp., *Pista australis* n. sp., *P. sinusa* n. sp., *P. turawa*, n. sp., *Reteterebella aloba* n. sp. and *Terebella maculata* n. sp., and the following new combination *Longicarpus modestus*.

A full description of all Australian species of this subfamily is given except when a recent description is available.

HUTCHINGS, P.A. and C.J. GLASBY, 1988. The Amphitritinae (Polychaeta: Terebellidae) from Australia. Records of the Australian Museum 40(1): 1-60.

This paper describes the Australian Amphitritinae (F. Terebellidae) and concludes the description of the Australian terebellid fauna (Hutchings & Glasby, 1986a,b, 1987). To date, no species of the subfamily Artacaminae have been found in Australia. We have attempted to examine all the material that is available and have borrowed the complete holdings of terebellids from all museums in Australia. However, material from certain areas of Australia is lacking, especially from shelf or deeper waters, and we anticipate that the terebellid fauna will continue to expand.

In this paper we discuss several genera not previously described from Australia, including several of the abbranchiate genera. Hesse (1917) placed these genera in the Amphitritinae rather than in the Polycirrinae because of the arrangement of uncini in double rows on at least some segments. The majority of these genera (*Baffinia*, *Lanassa*, *Laphania*, *Phisidia*, *Proclea*, *Spinospaera* and *Stschapovella*), contain few species and these are often poorly described. Many are deep water species, which have not been recorded since their original description. Considerable problems exist within these genera but a generic revision is beyond the scope of this paper. We have therefore followed

Fauchald's (1977) generic definitions of the abbranchiate genera, for the description of several new species from shallow or intertidal areas in southern Australia. However we believe that the current definitions of species in these genera, which are largely based on the structure of the notosetae, pose many problems as most of these setae, when viewed under oil emersion, are denticulate to some degree.

Clarification of the setal structures in the abbranchiate genera, using scanning electron microscope techniques, is urgently needed as is the defining of the presence or absence of lateral lobes. In some species examined, described in genera characterised as having lobes, these structures were mere ridges not comparable in structure to those found, for example, in *Pista* or *Loimia*. Any generic revision must consider these points. However, in all genera of terebellids, notosetae must be examined under oil emersion in order to elucidate their fine structure.

Prior to this study, several widely distributed or so called 'cosmopolitan species' had been reported from Australia (Day & Hutchings, 1979). Examination of type material or material from the type locality has

revealed in many cases that the Australian material was not the same and these species have now been described as new. Some of these new species have names derived from aboriginal words which were found by consulting the following sources: a compilation of 'Australian Aboriginal Words and Place Names and Their Meanings' by Endacott (1924) and 'The Aborigine of South Eastern Australia, as They Were' by Massolin (1971).

A discussion of the biogeography of Australian terebellids is given by Hutchings & Glasby (in press) which is largely based on this paper and previous papers on the Polycirrinae and Thelepininae (Hutchings & Glasby, 1986b, 1987).

In this paper, we have examined a considerable amount of material from Western Port, Port Phillip Bay (PPBES, CPBS) and Bass Strait collected by the Museum of Victoria. In the case of type material or individual records we have given latitude and longitude but in many cases we have just quoted station numbers. Full station data including latitude, longitude, depth, sediment, date and method of collecting can be found in the following two technical papers: Poore (1986) for Port Phillip Bay and Western Port) and Wilson & Poore (1987) for Bass Strait.

The following abbreviations have been used.

AHF	Allan Hancock Foundation, Los Angeles
AM	Australian Museum, Sydney
BMNH	British Museum of Natural History, London
CAS	California Academy of Sciences, California
CSIRO	Commonwealth Scientific and Industrial Research Organization, North Beach, Perth
HZM	Zoologisches Institut und Zoologisches Museum der Universität, Hamburg
MCZ	Museum of Comparative Zoology, Harvard
MNHN	Museum D'Histoire Naturelle, Paris

MPW	Muzeum Przyrodnicze, Wroclaw
NMV	Museum of Victoria, Melbourne
NT	Northern Territory Art Gallery and Museum, Darwin
QM	Queensland Museum, Brisbane
QEM	Queensland Electricity Generating Board, Brisbane
SAM	South Australian Museum, Adelaide
SSM	Naturhistoriska Riksmuseet, Stockholm
TASM	Tasmanian Museum, Hobart
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UUZM	Uppsala Universitets Zoologiska Museum, Uppsala
WAM	Western Australian Museum, Perth
ZMA	Zoologisch Museum, Amsterdam
ZMB	Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin
ZMC	Zoologisk Museum, Copenhagen

Systematics

Amphitritinae

Amphitritae Savigny, 1820: 71.

Terebellacea Grube, 1850: 325–328.

Prostomium compact. Branchiae present or absent, if present, 1–3 pairs typically branched or tufted. Lateral lobes present or absent on anterior segments. Peristomium may be expanded to form a lobe. Notopodia present for a variable number of segments; notosetae smooth or serrated. Neuropodia present for a large number of segments, uncini avicular, short or long handled, or uncini with teeth arranged in a vertical row. Uncini initially arranged in single rows on thorax but then arranged in double rows posteriorly. Distinct ventral glandular pads present on anterior thoracic segments.

Key to the Australian genera of Amphitritinae

(after Fauchald, 1977)*

1. Branchiae absent 2
- Branchiae present 5
2. Thoracic setigers, 17 or less 3
- Thoracic setigers, more than 20 *Baffinia*
3. Thoracic setigers, 17 pairs, notosetae of setiger 12 enlarged *Arranooba*
- Thoracic setigers, less than 17 pairs, notosetae of setiger 12 not enlarged 4
4. 15 thoracic setigers; notosetae finely denticulated *Lanassa*
- 14 thoracic setigers; some notosetae distinctly pectinated *Phisidia*
5. Notosetae, at least some, with marginally serrated tips 6
- Notosetae all with smooth tips 11

* This key is artificial and does not imply any phylogenetic relationships.

6. Thoracic uncini all avicular 7
- Thoracic uncini, anteriorly long handled with heavily chitinised shafts 10
7. Lateral lobes present *Amphitrite*
- Lateral lobes absent 8
8. Notopodia from segment 3, neuropodia from segment 5 *Neoleprea*
- Notopodia from segment 4, neuropodia from segment 5 9
9. 2 pairs of branchiae *Amphitritides*
- 3 pairs of branchiae *Terebella*
10. 16 pairs of notopodia *Hadrachaeta*
- 23 pairs of notopodia *Longicarpus*
11. Uncini with teeth in a single row *Loimia*
- Uncini with teeth in 2 or more rows consisting of main fang and a crest of smaller teeth 12
12. Anterior uncini short handled 13
- Anterior uncini long handled 17
13. Uncini present from segment 5 (setiger 1) *Reteterebella*
- Uncini present from segment 4 (setiger 2) 14
14. Lateral lobes absent *Nicolea*
- Lateral lobes present 15
15. Lateral lobes present as small lappets on segments 2, 3 and 4 *Eupolymnia*
- Lateral lobes absent on segments 2 and 4 16
16. Peristomial lateral lobes present, lateral lobe also present on segment 3. *Lanice*
- Peristomial lateral lobes absent, lateral lobes present on segment 3 *Lanicola*
17. Lateral lobes present on segment 3 and sometimes on peristomium *Lanicides*
- Lateral lobes present on segments 2 to 4 and sometimes on peristomium *Pista*

***Amphitrite* Müller, sensu lato**

Amphitrite Müller, 1771: 8.—Hessle, 1917: 185.—Fauvel, 1927: 244–245.

Amphiro Montagu, 1808 in McIntosh, 1922: 107.

Neoamphitrite Hessle, 1917: 178–179.—Berkeley & Berkeley, 1952: 85.—Kritzler, 1984: 34.

Branchiae 3, rarely 2, pairs from segment 2; dendritically branched or filiform arising from a basal stump or distinct stalk. Lateral lobes present on anterior segments. Notopodia from segment 4, 17–25 pairs; notosetae distally serrated. Neuropodia with uncini from segment 5 (setiger 2) arranged in double rows in posterior thorax, either as an interlocking “zipper” or in 2 distinct rows. Nephridial papillae from segment 3.

Type species. *Amphitrite cirrata* Müller, 1771 by monotypy.

Comments. We have followed Fauvel’s (1927) definition of *Amphitrite* which synonymises

Neoamphitrite Hessle, 1917 with *Amphitrite*. The two genera can be differentiated, according to Hessle, by the form of the nephridia and the form of the branchiae, which in *Neoamphitrite* are richly branched with a distinct stalk and in *Amphitrite*, filiform with a very reduced stalk. We believe that these two types of branchiae are not sufficiently different to constitute a good generic character. For example, the length of the branchial stem is quite variable within and between specimens in our material, with the larger specimens often having a better developed stem. In addition some species such as *Amphitrite robusta* Johnson, 1901 have branchiae which are intermediate between those of *Amphitrite* sensu stricto and those of *Neoamphitrite*. The other distinguishing character used by Hessle is the form of the nephridia which he used as a generic character to separate terebellid genera. The dissection and the segmental affinities of the nephridia are difficult to discern in small specimens or poorly preserved

individuals. The majority of workers since Hesse (1917) have ignored the segmental affinities of the nephridia and most diagnoses of terebellids genera described since 1917 lack details of these structures. When a comprehensive revision of the family is undertaken, the usefulness of this character should be reassessed. It may be that internal morphology is more conservative than external soft structures (i.e. branchiae), and that the arrangement of nephridia will prove to be an important generic character. Another character which should be investigated, is the precise arrangement of uncini in the posterior thorax.

Fauchald (1977) described the genus *Amphitrite* as lacking lateral lobes, however Hesse (1917) clearly stated lateral lobes are present, although the original diagnosis of the genus by Müller (1771) does not mention lateral lobes at all. Hesse's definition is followed here. It is unclear as to the source of Fauchald's (1977) definition of the genus.

The genus *Amphitrite* is represented by two species in Australian waters, *A. pachyderma* n. sp. and *A. oculata*. *Amphitrite pachyderma* n. sp. is well represented on the east coast of Australia, whereas *A. oculata* Hesse, 1917 has been found only from One Tree Island, Great Barrier Reef. *Amphitrite modesta* (Quatrefages, 1865) described from Jervis Bay, New South Wales and also recorded by Whitelegge, 1889 is synonymous with *Longicarpus glandulus* Hutchings & Murray, 1984 and is here redescribed as *Longicarpus modestus*. *Amphitrite rubra* (Risso, 1828), recorded from South Australia to Queensland by various authors (see Day & Hutchings, 1979), has been referred to either *Amphitrite pachyderma* or *Longicarpus modestus*. A type of *A. rubra* has been examined (MNHN UB 392) and the specimen does not belong in the genus *Amphitrite*. A full description of this supposedly widely occurring species is being prepared by Hutchings and Glasby.

Key to the Australian species of *Amphitrite*

1. Notopodia, 23 pairs; branchiae, 3 pairs, dendritically branched ... *A. pachyderma*
- Notopodia, 17 pairs; branchiae, 3 pairs, unbranched *A. oculata*

Amphitrite oculata Hesse

Fig. 1a–d

Amphitrite oculata Hesse, 1917: 186.—Fauvel, 1936: 80–81.—Okuda & Yamada, 1954: 193–194, fig. 8.—Imajima & Hartman, 1964: 336.

Material examined. Queensland: Great Barrier Reef, One Tree Island, 23°30'S, 152°05'E, 1(AM W200139), 1(AM W200143), 1(AM W200142), 1(AM W200145), 2(AM W200141), 1(AM W200144), 1(AM W200140), 1(AM W200146), specimens range in size from 12.2 mm long, 1.5 mm wide for 57 segments to 16.2 mm long, 2.0 mm wide for 61 segments.

Japan: Misaki, SYNTYPES 1(UUZM 169a), 1(UUZM 169b) coll. S. Bock 23.4.1914, 25.4.1914 respectively.

Comments. The syntypes of *Amphitrite oculata* closely resemble the Australian material in all respects except for the distribution of eyespots, which is uniform across the dorsum of the peristomium in the former but concentrated in a distinct patch laterally in the Australian specimens. The setae of the Australian specimens resemble those of the syntypes (Fig. 1a–d). This is the first record of this species in Australian waters, previously known only from Japan.

Habitat. Found in shallow waters in Japan; and in coral substrates in the lagoon at One Tree Island.

Distribution. Australia (One Tree Island). Japan (Misaki, Fujitas Kolonie, Mori, Seto, Matsushima Bay, Isozaki).

Amphitrite pachyderma n. sp.

Fig. 1e–h

Amphitrite rubra.—Rullier, 1965: 195.—Stephenson et al., 1970: 491; 1974: 113.—Hutchings, 1977: 16 (in part). Non Risso, 1826.

Material examined. HOLOTYPE: Queensland: Moreton Bay 20°26'S, 147°05'E, Stn III B4, 2.4 kms south of South West Rocks, Peel Island, (AM W5100); complete, 109 segments, 48 mm long, 7.0 mm wide. PARATYPES: Queensland: Moreton Bay 1(AHF Poly 1464), (AM W7091); Gladstone, Auckland Creek 23°51'S, 151°16'E, 1(BMNH ZB 1986.61); Calliope River 1(USNM 99965), 1(AM W198246), 2(AM W198247). Paratypes range in size from about 17.5 mm long, 1.9 mm wide for 80 segments to a posteriorly incomplete specimen 3.6 mm wide.

Additional material examined. New South Wales: Georges River, Tom Uglys Bridge 6(AM W7889), 3(AM W7797); Botany Bay, Towra Point 1(AM W7528).

Description. Body robust, widest at midthorax, abdomen short gradually tapering. Tentacular lobe short, collar-like. Buccal tentacles largely missing, remaining ones filiform, grooved. Eyespots absent. Peristomium about equal in length to segment 2 dorsally and laterally. Lower lip divided by deep transverse groove to form shelf-like outer region, dome-shaped inner region. Inner lips retracted within oral cavity.

Branchiae paired on segments 2–4, arise from anterior edge of segments, just above line of notopodia, those on segment 3 inserted slightly laterally to those on segments 2 and 4; branchiae dendritically branched with very thick main stem, short, thick secondary branches, mass of short, stumpy terminal branches, with short but distinctive stalks. Branchiae decrease in size posteriorly, those on segment 3, on left side very small, presumably regenerating. Lateral lobes paired on segments 2–4, distinct thickened flaps; each pair equally well developed, arranged in an increasingly dorsal



Fig.1. *Amphitrite oculata*. a. short notoseta from setiger 12, scale is 0.1 mm. b. long notoseta from setiger 12, scale is 0.1 mm. c. uncinus from midabdomen, scale is 0.01 mm. d. uncinus from midabdomen, scale is 0.01 mm. *Amphitrite pachyderma* n.sp., holotype. e. ventrolateral view of anterior body, scale is 1 mm. f. long notoseta from setiger 3, scale is 0.1 mm. g. short notoseta from setiger 3, scale is 0.1 mm. h. uncinus from segment 13, scale is 0.01 mm.

position posteriorly. Segments 2 and 3 ventrally thickened, resembling modified ventral pads, segment 4, extremely reduced ventrally (Fig. 1e).

Notopodia from segment 4, present on following 23 segments; podia short, rectangular, retracted in some segments. Notosetae arranged in 2 tiers in each fascicle; long narrow-winged, distally hispid capillaries, shorter capillaries of the same type (Fig. 1f–g). Neuropodia from segment 5 (setiger 2), continue to pygidium; podia elongate, low ridges decreasing in length posteriorly from midthorax; dorsal end of podia marked by small papilla in abdominal segments. Uncini with delicate subrostral guard visible under high power, strong, hooked anterior basal attachment point (Fig. 1h). Dental formula, MF:7–9:7–10:16–22, with most distal row somewhat irregular, perhaps consisting of 2 rows. Uncini arranged in single row to segment 10, then in an alternating row, arranged face to face until segment 44 when uncini are again arranged in single rows to the pygidium.

Midventral glandular pads on segments 5–15, all similar sized; thereafter shallow, segmented glandular groove to pygidium. Nephridial papillae on segments 3–9, first 3 pairs elongate, remainder very flat and small; base of papillae on segments 6–9 swollen, forming glandular discs.

Holotype gravid female.

Variation. The material examined shows the following variation: branchiae vary considerably in overall size and in length of terminal filaments, lateral lobes thickened or lamellae like. Notopodia from segment 3, 22–24 pairs. Uncini arranged in an alternate row from segment 11, then in single row from segment 40–44 to the pygidium. Dental formula MF:5–7:6–8:15–25, with most distal row possible consisting of 2 rows of teeth. Midventral glandular pads from segment 5–15 or 16. Nephridial papillae present on segments 3–9 in all paratypes; none with swollen glandular discs at base of papillae.

Comments. We have examined a wide range of different sized specimens of *Amphitrite pachyderma* n.sp. The number of pairs of notopodia is commonly 23 pairs with a range of 22 to 24. There appears to be no correlation between the number of pairs of notopodia and the size of the animal. Very few species of *Neoamphitrite*/*Amphitrite* have this number of notopodia, although ranges of numbers are rarely given in the literature. Only *A. chloraema* (Schmarda, 1861) which has 22 pairs according to Ehlers, 1901, *A. modesta* (Quatrefages, 1865), now *Longicarpus modestus*, which has 21 or 22 pairs and *Neoamphitrite figulus* (Dalyell, 1853) which has 24 pairs according to Hessle, 1917, fall within the range exhibited by the Australian species. Of these, *L. modestus* differs in having anterior uncini with well-chitinised shafts and *A. chloraema* differs from *A. pachyderma* in the shape of the uncini. An uncinus of *A. chloraema* figured by Schmarda lacks a subrostral

ligament as well as a well defined heel like those of the Australian specimens.

A specimen of *N. figulus* (AM W9131) from Maine, identified by Pettibone, was compared to our material. It differs in having uncini arranged in single rows from segment 30 to the pygidium and in having many more pairs of nephridial papillae which are very small and difficult to count but present on at least segments 3 to 15.

Amphitrite pachyderma n. sp. differs from the other species of *Amphitrite* occurring in Australia, *A. oculata*, in the number of pairs of notopodia present and in the form of the branchiae, which are unbranched in the latter species.

Etymology. Specific name derived from the Greek adjective, *pachys*, thick and *derma*, skin referring to the thickened ventral pads on segments 2 and 3.

Habitat. Sheltered bays and estuaries, 2–15 m, sand-muddy sediment, sometimes with shell fragments.

Distribution. New South Wales, Queensland.

Amphitritides Augener

Amphitritides Augener, 1922: 47.—Fauchald, 1977: 130.

Branchiae 2 pairs, on segments 2 and 3, stalked. Lateral lobes absent. Notopodia from segment 4, continue for variable number of segments; notosetae distally serrated. Neuropodia with uncini from segment 5 (setiger 2), arranged in double rows, face to face on some thoracic and abdominal segments.

Type species. *Terebella gracilis* Grube, 1860 by original designation.

Comments. The two new species of *Amphitritides* described here, increases the number of species belonging to this genus to four. The type species, *A. gracilis* (Grube, 1860), was described from the Mediterranean Sea and *A. bruneocomata* (Ehlers, 1887) was described from the Caribbean, south of Florida. The two species described in this paper represent the first records of this genus in Australian waters.

Key to the Australian species of *Amphitritides*

1. Notopodia continue almost to pygidium; nephridial papillae on segments 3 and 6–10. *A. harpa*
 —Notopodia, 20 pairs, nephridial papillae on segments 3 and 6–13. *A. ithya*

Amphitritides harpa n. sp.

Fig. 2a–f

Material examined. HOLOTYPE: Queensland: Great Barrier Reef, Stn 9 Eclipse Island, 18° 46' S, 146° 33' E (AM

W200344) posteriorly incomplete, 81 segments, 1.5 mm wide. PARATYPE: Great Barrier Reef, One Tree Island 23°30'S, 152°05'E I(AM W200345); complete, about 100 segments, 19 mm long, 1.0 mm wide.

Description. Body widest anteriorly, abdomen very long, gradually tapering, coiled. Tentacular lobe collar like. Buccal tentacles long, filiform, grooved. Eyespots red, arranged in small patch laterally, at the base of posterior tentacular lobe. Peristomium indistinct dorsally, ventrally forming a crescent shaped lower lip, partially covering large, padlike inner lip. Branchiae dendritically branched with

short, thick stalk; 2 pairs on segments 2 and 3, anterior pair arise just above line of notopodia, posterior pair dorsally displaced, arise from posterior edge of segment. Lateral lobes absent (Fig. 2a).

Notopodia from segment 4, continue for at least 78 segments, to near pygidium; podia short, triangular, sub-rounded, reduced posteriorly to small tubercle. Notosetae anteriorly very long, narrow-winged capillaries, slightly hirsute along 1 edge, with very short, faintly hispid tip (Fig. 2b,c), 2 lengths of setae present; posteriorly notosetae sickle-shaped capillaries, wingless, subdistally expanded with

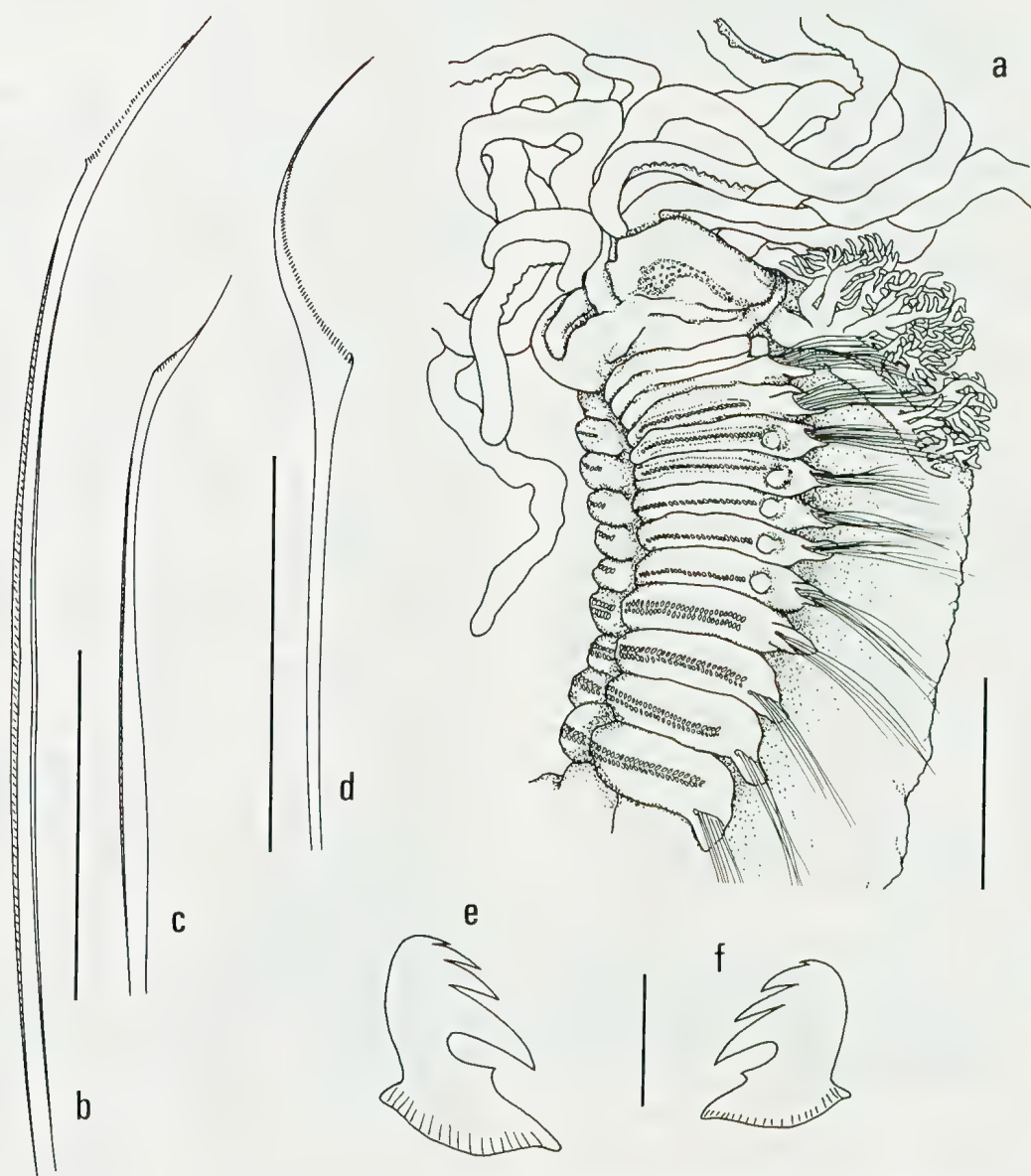


Fig.2. *Amphitritides harpa* n. sp., holotype. a. ventrolateral view, anterior body, scale is 1 mm. b. long notoseta from notopodia 6, scale is 0.1 mm. c. short notoseta from notopodia 6, scale is 0.1 mm. d. notoseta from midabdomen, scale is 0.1 mm. e. uncinus from midthorax, scale is 0.01 mm. f. uncinus from midabdomen, scale is 0.01 mm.

longer hispid region distally, all similar in length (Fig. 2d). Neuropodia from segment 5 (setiger 2), present on all following segments; podia long, low ridges, similar in size throughout first half of body, then podia decreases in length gradually over remaining segments. Uncini with sharply pointed, subrostral ligament and slightly curved base (Fig. 2e,f), dental formula MF:3-4:6-9:9-12; arranged in single rows to segment 10, thereafter uncini arranged in double rows, face to face.

Midventral glandular pads occur on segments 2-12, thereafter reduced to glandular streak, initially deep, becoming shallow, continues to pygidium. Nephridial papillae small, flat, occur on segment 3 just lateral to first pair of branchiae and on segments 6-10 at the dorsal end of the neuropodial tori.

Variation. Paratype specimen complete, pygidium with 6 large papillae arranged almost equidistantly around perimeter, ventral pair separated slightly further. Branchiae very small, dendritic, with few branches. Notopodia continue to near pygidium, abdominal ones with reduced complement of notosetae. Midventral glandular pads on segments 2-11. Nephridial papillae arranged as for holotype, although very small, inconspicuous.

Comments. *Amphitritides harpa* n. sp. differs from the other species of *Amphitritides* from Australia, *A. ithya* n. sp., in the number of pairs of notopodia present, the form of the notosetae and uncini and the number of pairs and position of the nephridial papillae. For details of these characters see description of *A. ithya* n. sp. It most closely resembles *A. bruneacomata* (Ehlers, 1887) in having a large number of pairs of notopodia, but differs from this species in having peculiar sickle-shaped, subdistally expanded notosetae in posterior segments and the second pair of branchiae dorsally displaced unlike *A. bruneacomata* in which the first pair appears dorsally displaced. The sickle-shaped notosetae resemble those found in the genus *Spinospaera* Hesse. *Amphitritides harpa* differs from *A. gracilis* (Grube, 1860) most noticeably in the number of pairs of notopodia viz. 17 or 18 according to Grube and 17-19 according to Fauvel (1953).

Etymology. Specific name from the greek noun, *harpe*, sickle, referring to the sickle-shaped posterior notosetae.

Habitat. Found subtidally, in soft sediment, in between reefs.

Distribution. Queensland.

Amphitritides ithya n. sp.

Fig. 3a-d

Terebella pterochaeta.—Hartmann-Schröder, 1979: 148.
Non Schmarda, 1861.

Material examined. HOLOTYPE: Queensland: Port Denison 20°03'S, 148°15'E (AM W200338), posteriorly incomplete, 61 segments, 2.3 mm wide. PARATYPE:

Queensland: Gulf of Carpentaria, west of Topsy Creek, 15°28.5'S, 140°53.2'E 1(AM W200339), complete, 77 segments, 13.2 mm long, 1.3 mm wide.

Additional material examined. Western Australia: Broome, Mangrove Point 1(NTM W2107), (HZM P16624); Port Hedland (HZM 16625); Cable Beach 2(NTM W22496). Northern Territory: East Point 1(NTM W2825), 1(NTM W2794).

Description. Body coiled, widest anteriorly, gradually tapering posteriorly. Tentacular lobe collar like. Buccal tentacles largely missing. Eyespots small, red, arranged in broad band across posterior tentacular lobe, most numerous laterally. Peristomium distinct, slightly longer than succeeding segment dorsally and laterally, ventrally forming pair of thin lower lips; pair of crescent-shaped inner lips protrude from oral cavity. Branchiae richly branched, short stalk, 2 pairs on segments 2 and 3, arise just above line of notopodia. Lateral lobes absent (Fig. 3a).

Notopodia from segment 4, 20 pairs; podia short, rectangular, reducing in size slightly posteriorly. Notoetae of 2 lengths, arranged in 2 tiers, long winged capillaries, distally hispid, short capillaries similarly hispid and winged (Fig. 3b,c). Neuropodia from segment 5 (setiger 2), present on all segments posteriorly; podia low ridges throughout, first 6 pairs of neuropodia positioned laterally, next several pairs longer, extending onto ventrum just short of ventral pads, then neuropodia decreasing in length gradually posteriorly. Uncini with delicate pointed, upright subrostral ligament and convex base (Fig. 3d); dental formula MF:3:4-6:6-9, throughout; uncini arranged in single rows to segment 10, thereafter in double rows, face to face.

Midventral glandular pads on segments 2-13, thereafter glandular streak in shallow groove to pygidium. Nephridial papillae flat, paired, present on segments 3, 6-14; first pair arise just lateral to branchial stalk, remainder arise from anterior base of notopodia.

Variation. Paratype with many buccal tentacles, filiform, grooved, longest extending to pygidium. Eyespots fewer, scattered irregularly across dorsum. Notopodia only present to segment 19. Uncini arranged in double rows to near pygidium. Nephridial papillae on segments 3, and 6-13. Structure of pygidium difficult to discern.

Comments. *Amphitritides ithya* n. sp. differs from *A. harpa* in having far fewer pairs of notopodia, notosetae of one type (although different lengths), uncini with an upright subrostral ligament rather than one anteriorly directed and nephridial papillae on segments 3 and 6 to 13 or 14. These papillae arise from the anterior base of the notopodia in *A. ithya* unlike *A. harpa* which has nephridial papillae on segments 3 and 6 to 10, and located at the dorsal end of the neuropodial tori.

The material identified by Hartmann-Schröder (1979) as *Terebella pterochaeta* is referred to *A. harpa*.

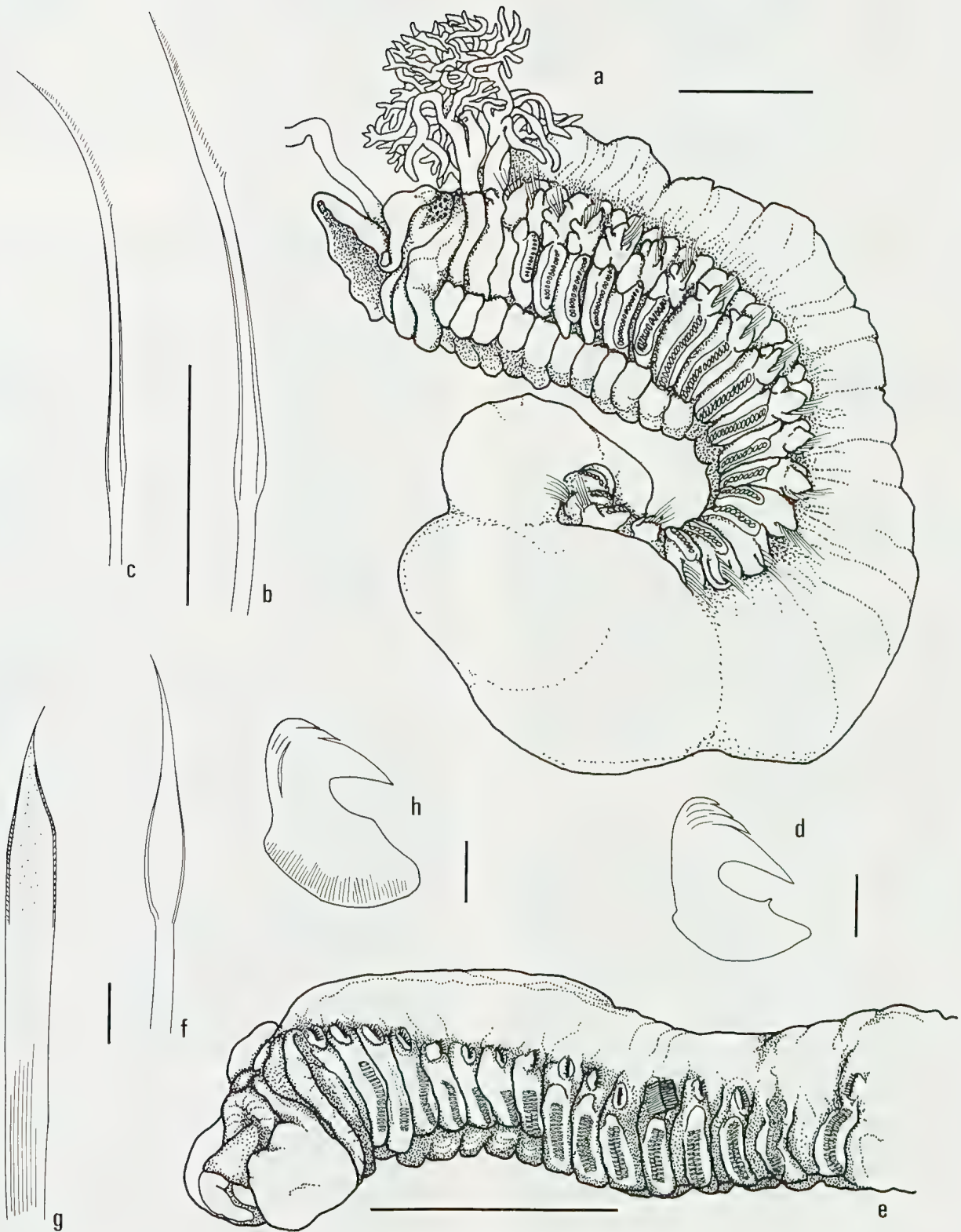


Fig.3. *Amphitritides ithya* n. sp., holotype. a. ventrolateral view of anterior body, scale is 1 mm. b. long notoseta from notopodia 12, scale is 0.1 mm. c. short notoseta from notopodia 12, scale is 0.1 mm. d. uncinus from segment 15, scale is 0.01 mm. *Arranooba booromia* n. g., n. sp., holotype. e. lateral view of anterior body, scale is 1 mm. f. notoseta from setiger 12, scale is 0.01 mm. g. notoseta from setiger 12, scale is 0.01 mm. h. uncinus from setiger 12, scale is 0.01 mm.

Terebella pterochaeta Schmarda, was originally described from southern Africa. Material from southern Africa (HZM PE 1255, PE 1256, PE 1189, V 8770) has been examined and has 29 to 30 pairs of notopodia whereas *A. harpa* has 19 or 20 pairs of notopodia. Type material of *T. pterochaeta* has however, not been located.

Etymology. Specific name derived from the Greek adjective *ithys*, straight, upright, referring to the angle of the subrostral ligament of the uncini.

Habitat. Paratype collected from about 25 m, details of substrate unknown, no habitat data available for holotype.

Additional material from East Point was collected from rocks embedded in mud and from Cable Beach from the low water mark under stones and encrusting algae.

Distribution. Western Australia (Broome), Queensland (Port Denison, Gulf of Carpentaria), Northern Territory (East Point).

Arranooba n. gen.

Prostomium compact, branchiae absent, lateral lobes present, well developed on peristomium, and segments 2 and 3. Notopodia begin on segment 4 and continue to segment 20 (17 pairs of notopodia). Notosetae of 2 types, narrow-winged capillaries with smooth tips and capillary setae with margins inwardly curved to form a quill-shaped setae. Setae of segment 15 (setiger 12), considerably enlarged and thickened. Neuropodia from segment 5 (setiger 2) and continue to pygidium. Uncini avicular, initially arranged in single rows and then arranged in double rows from uncinigerous segment 7 to the end of the thorax, thereafter in single rows.

Type species. *Arranooba booromia* n.sp.

Comments. *Arranooba* belongs to the abbranchiate group of Amphitritinae, which include *Baffinia* Wesenberg-Lund, *Lanassa* Malmgren, *Laphania* Malmgren, *Leaena* Malmgren, *Phisidia* Saint-Joseph, *Proclea* Saint-Joseph, *Spinospaera* Hessle, and *Stschapovella* Levenstein. These genera are distinguished by such features as the number of pairs of notopodia, type of notosetae, where the neurosetae begin and the presence or absence of lateral lobes. None of the described genera has the combination of features which *Arranooba* possesses. *Laphania* has 17 pairs of notopodia, but lacks lateral lobes and the neurosetae do not begin until segment 8 (setiger 7). *Leaena* appears to be the closest genus to *Arranooba* but only has 16 pairs of notopodia, and lateral lappets are present together with a transverse ridge across the dorsum. Certainly some species of *Leaena* examined have very poorly defined lateral lobes, whereas in *Arranooba* they are very well defined. In no genus of Amphitritinae have any notopodia been recorded in which some setae are considerably enlarged as in *Arranooba*.

As many abbranchiate species are small, it is likely that additional species and genera will be found in Australia. Most representatives of these genera occur in the polar regions or in deep water, although this Australian study has recorded several from shallow depths.

The generic name *Arranooba* (gender feminine) is an aboriginal word for a place in Western Australia.

Arranooba booromia n. sp.

Fig. 3e-h

Material examined. HOLOTYPE: Western Australia: Abrolhos Group, Rat Island 16°24'S, 123°07'E, reef crest 1 m in dead coral rubble (AM W200429). Complete specimen, 6 mm in length and 1.5 mm in width.

Description. Preserved specimen pale yellow with golden setae, in fine chitinous tube.

Prostomium compact. Single short buccal tentacle remaining. Eye spots absent. Lateral lobes well developed on peristomium, segments 2 and 3, all projecting forwards and encompassing the prostomium. Peristomial lateral lobe rectangular, segment 2 with large rectangular glandular lobe meeting midventrally, largest of the 3 lobes. Segment 3 with small rounded semi-circular lobe overlapping the base of the one occurring on segment 2. All pairs of lateral lobes very tightly overlapping each other. Branchiae absent (Fig. 3e).

Notopodia begin on segment 4, continue for 17 segments, small rounded podia, except for podia of segment 15 (setiger 12), which is considerably enlarged with very well-developed bundle of golden setae. Notosetae of 2 types, very broad-bladed, narrow-winged capillaries with drawn out fine smooth tips, blades with fine surface striations, 2 lengths of this type of seta present; other type of seta with margins enrolled to form a blunt quill type seta. Setae of setiger 12 similar to other setae but much thicker (Fig. 3f,g), more setae present than in typical bundle of setae.

Neuropodia begin on segment 5 (setiger 2), continue to pygidium. Length of uncinal row longer on first 3 uncinigerous segments than subsequent ones. Uncini avicular (Fig. 3h) with the following dental formula MF:4-5:5:6 or MF:6:6:5:α. Uncini initially arranged in single rows, then arranged in double rows from uncinigerous segment 7 to end of thorax, and then uncini again arranged in single rows to the pygidium.

Abdominal uncini arranged on elongate erect rectangular tori with margin slightly expanded giving a globular appearance.

Ventral pads well developed, segmentally demarcated on anterior thorax, from about setiger 12 onwards, width of ventral pad declines and then rapidly tapers into a narrow ventral stripe which then completely disappears. Ventral pads not markedly glandular.

Nephridial papillae absent, and coelom devoid of any gametes.

Etymology. The specific name is an aboriginal word for wind. The Abrolhos Islands, the type locality for the species, are known for the strong prevailing winds which blow onto the treeless islands for most of the year.

Habitat. Found in coral rubble in depths of 2–3 m.

Distribution. Western Australia (Rat Island, Abrolhos group).

Baffinia Wesenberg-Lund 1950 emended
Fournier & Barrie, 1984

Baffinia Wesenberg-Lund, 1950: 53–54.—Fournier & Barrie, 1984: 1397–1401.

Abbranchiate Amphitritinae, lateral lobes absent, ventral glandular shield well developed on some anterior segments. Notopodia from segment 4, continuing to near posterior end, notosetae of 2 types, limbate with serrated tips in anterior setigers becoming broadly geniculate, flail tipped with strongly serrated blades from about segment 13–15 (setiger 10–12), to end of body. Neuropodia present from segment 5 (setiger 2) to almost the pygidium, uncini uniformly short, avicular with 4–5 rows of small teeth above the main fang, uncini arranged in single rows initially, then in double rows for 20 or more setigers, then arranged in single rows for remaining setigers.

Type species. *Baffinia multisetosa* Wesenberg-Lund, 1950, by original designation.

Comments. Fournier & Barrie (1984) have recently reviewed this previously monospecific genus and synonymised *Terebella hesslei* Annenkova, 1924 with *B. multisetosa*. We have emended the generic diagnosis to accommodate our new species from Victoria, to allow some variation in the segment on which the neurosetae are arranged in double rows and the segment on which the notosetae change from simple to flail tipped setae. Within the Amphitritinae only two genera, *Baffinia* and *Proclea* Saint-Joseph have notosetae changing in structure along the body. *Baffinia* has notopodia from segment 4 and neuropodia from segment 5, whereas *Proclea* has notopodia from segment 4 and neuropodia from segment 6. Thus *Baffinia biseriata* n. sp. clearly belongs to *Baffinia* which is also characterised by uncini arranged in double rows for many segments. In contrast *Proclea* has uncini in double rows only from segments 11–19. We agree with the comments made by Fournier & Barrie (1984) that the genus may need to be reconsidered when generic revisions of some other poorly known terebellid genera are undertaken.

Baffinia biseriata n. sp.

Fig. 4a–d

Material examined. HOLOTYPE: Victoria: Gabo Island 37°34'S, 149°55'E (AM W200437) on vertical rock face in

among dense upper storey of the algae *Phyllospora*, with sparse red algae underneath, 6 m, complete specimen, 69 segments, 15 mm in length and 1.5 mm wide at anterior end tapers towards the pygidium. PARATYPES: Victoria: south south-east side of Gabo Island 23 m, on large boulders in among sponges and ascidians, 1(AM W200438), 1(AHF Poly 1465); Gabo Island, off Monument Bay in 18–20 m, boulder fauna (USNM 99966). New South Wales: Bass Point 34°36'S, 150°54'E, 18–20 m (BMNH ZB 1986.62). Paratypes posteriorly incomplete specimens, 10–15 mm in length and 1–1.5 mm in width.

Additional material examined. New South Wales: North Head off Sydney, 30 m, 6(AM W200439), 1(AM W200440).

Description. Preserved specimen colourless. Prostomium produced anteriorly, short sloping margins thickened from which buccal tentacles arise. Few buccal tentacles remain, thick and grooved. Prostomium ventrally appears as tongue-like projection with thickened margins. Eye spots absent. Branchiae absent. Lateral lobes absent but anterior margins of segments 2–4 are slightly thickened (Fig. 4a).

Distinct segmental ventral glandular pad present initially, continue to setiger 9, but then rapidly taper into narrow glandular streak which continues to pygidium. Anterior dorsum inflated.

Notopodia begin on segment 4, continue to pygidium, podia are small rounded protruberances. First 10 pairs of notopodia with 2 tiers of setae, consisting of 2 types, longest, broad-winged capillaries with long pointed tips, margins of wings minutely hirsute (Fig. 4b), shorter notosetae, wingless, with small flayed tips, prominent V-shaped supporting structure at the base of the flail (Fig. 4c). Subsequent notopodia after segment 13 (setiger 10) with 2 tiers of flail tipped notosetae (Fig. 4c). Basal part of the notosetal blade with well-developed chitinised V-shaped support which almost articulates with the shaft. Blade initially strongly serrated but then rapidly tapers into a long smooth tip.

Neuropodia begin on segment 5 (setiger 2), continue to pygidium. Neuropodia initially with long rows of uncini, surrounded by glandular material. Subsequently the neuropodia become shorter, less glandular, in far posterior have only 5–7 uncini per row. Uncini, arranged in single rows on first 6 neuropodia, subsequently uncini arranged in double rows face to face, this pattern continues until 19 segments from the pygidium, when the uncini are again arranged in single rows. Uncini avicular (Fig 4d) with strongly crested heads, dental formula in 1st neuropodia of MF:7-8:α:α:α:α:α, third neuropodia of MF:3:5:6-8:α, this formula maintained in posterior thoracic uncini.

Pygidium terminal with an anal rosette with small rounded protruberances around the margin.

Variation. Some of the paratypes are gravid, but gonopores are not evident. Paratypes exhibit some variation in the number of buccal tentacles

remaining. Some individuals have small gregarines attached to the surface epithelium. Within the additional material examined from North Head, New South Wales, there is some variation in the segment on which the neuropodial uncini become arranged in double rows; in 2 individuals this does not occur until the segment 12 (8th uncinigerous segment). These individuals are posteriorly incomplete and very small; at this stage we suggest this represents geographical variation in the species.

Comments. *Baffinia biseriata* n. sp. is only the second species of *Baffinia* to be described and it differs from *B. multisetosa* Wesenberg-Lund, 1950 in the arrangement of the neuropodial uncini. *Baffinia biseriata* n. sp. has the first 6 neuropodia (setigers 2 to 7) with uncini arranged in single rows, uncini are then arranged in double rows until 19 segments before the pygidium when they are arranged in single rows again. In contrast *B. multisetosa* with 70 segments, has uncini arranged in single rows on the first 8 neuropodia (setigers 2 to 9), then arranged biserially in facing rows on the next 21 neuropodia (setigers 10 to 30), reverting to uniserial arrangement again until almost to the end of the body. The last few segments apparently lack neuropodia (Fournier & Barrie, 1984).

Finally the structure of the notosetae differs in the

two species, with *B. biseriata* n. sp. having a well developed V-shaped supporting structure present at the base of the blade, such a supporting structure appears absent from those figured by Fournier & Barrie (1984).

Etymology. The specific name is derived from latin *bi*, double and latin *seriata*, row and refers to the numerous neuropodia with double rows of uncini.

Habitat. Found at depths of 6–23 m on boulders in among algae and sponges.

Distribution. Victoria (Gabo Island), New South Wales (Bass Point, North Head).

Eupolymnia Verrill

Eupolymnia Verrill, 1900: 660.

Amphitritoides Costa, 1862: 90.

Pallonia Costa, 1862: 88–89.

Polymnia Malmgren, 1867: 108.

Prostomium compact, branchiae, 3 pairs on segments 2, 3 and 4, branched. Lateral lobes present on segments 2, 3 and 4. Notopodia from segment 4, 17 pairs, with smooth-tipped notosetae. Uncini, avicular present from segment 5.

Type species. *Amphitrite nesidensis* delle Chiaje, 1828, designated by Hartman, 1959.

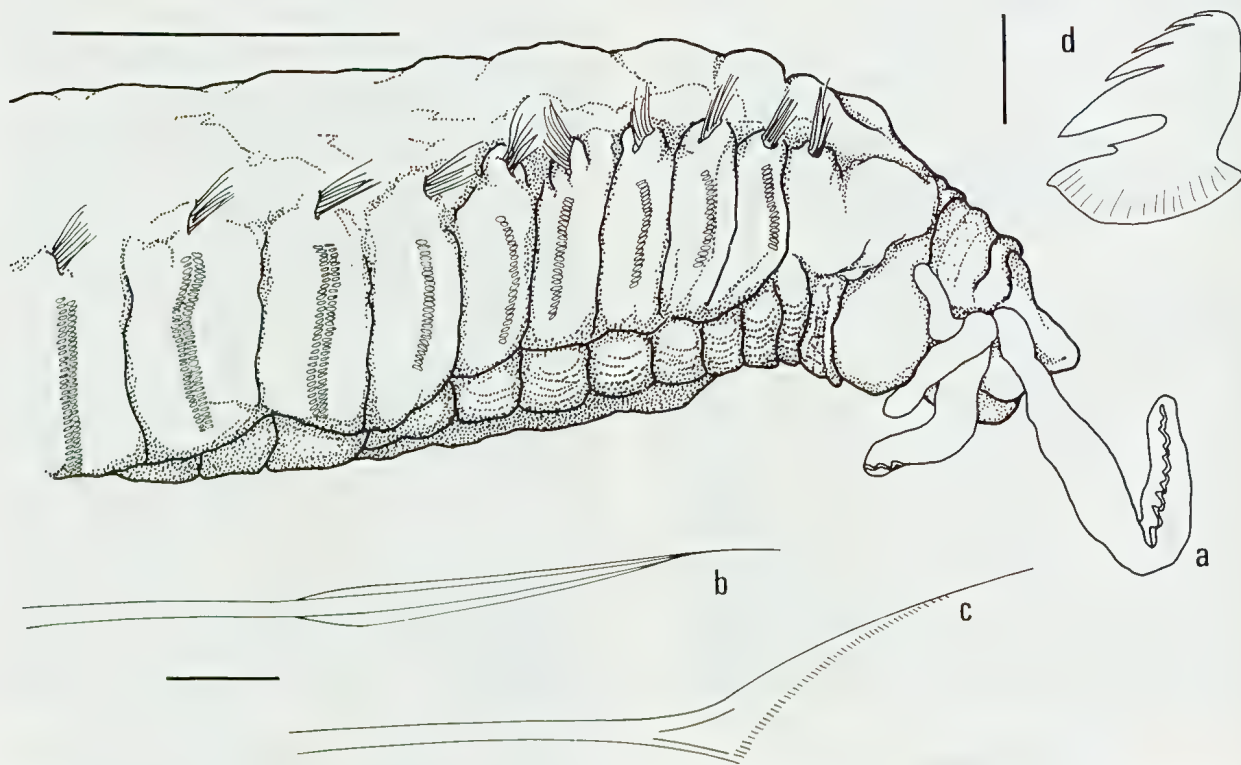


Fig. 4. *Baffinia biseriata* n. sp., holotype. a. lateroventral view of anterior body, scale is 1 mm. b. notoseta from setiger 3, scale is 0.1 mm. c. notoseta from setiger 3, scale is 0.1 mm. d. uncinus from unciniger 1, scale is 0.01 mm.

Comments. We have expanded the generic diagnosis to include the presence of lateral lobes on segment 4, as we do not regard the presence of an additional lobe on segment 4 of *Eupolymnia koorangia* n. sp. sufficient to warrant the erection of a new genus. *Eupolymnia koorangia* resembles *Eupolymnia* in all other respects.

Two species of *Eupolymnia* previously recorded from Australia, *E. nebulosa* (Montagu, 1818) and *E. trigonostoma* (Schmarda, 1861) do not occur in Australia.

***Eupolymnia koorangia* n. sp.**

Fig. 5a–c

Eupolymnia nebulosa.—Knox & Cameron, 1971: 38.—Hartmann-Schröder, 1979: 147; 1981: 57–58; 1982: 90; 1984: 44; 1985: 85; 1986: 58.—Hutchings & Murray, 1984: 96. *Non* Montagu, 1818.

Eupolymnia sp. Hartmann-Schröder 1987: 57

Material examined. HOLOTYPE: South Australia: Kangaroo Island, American River 35°48'S, 137°46'E (AM W14028) complete individual, 2 cm in length and 2.5 mm maximum width. PARATYPES: 1(BMNH ZB 1986.63), 1(USNM 99967), 1(AHF Poly 1466), 2(AM W200726), 2(AM W14027), all from American River inlet, Kangaroo Island.

Waterfall Beach (NMV F52591); Cockburn Sound (WAM 38-84); Rottnest Island, north-west West End (WAM 25-73); Thomson Bay (WAM 52-84); Cervantes (HZM P17166); Rockingham (HZM P17154); Albany (HZM P18104). South Australia: Ceduna (HZM P18105); Denial Bay (HZM P18106); Port Lincoln (HZM P18524); Wallaro, Point Riley (HZM P18664); Port MacDonnell (HZM P18663); Kangaroo Island, Shoal Bay (AM W200715), Emu Bay (AM W200713), Maston Point, American River (AM W200707), Penneshaw Jetty (AM W200712); Torrens Island (TASM K1020); Spencer Gulf (SAM E321); Sir Joseph Banks Group, cove at end of Reevesby Island (SAM E2002). Tasmania: Samphire Island off Flinders (TASM K1019); Eagle Hawk Neck (TASM K1018); Bass Strait: Stn 81, 92, 112, 117, 128, 133, 134, 135, 139, 153, 159, 163, 164, 167, 168, 169, 170, 174, 177, 179, 180, 185, 191, 194, 198, 203, 205, 219 (NMV unreg.). Victoria: Portland Harbour (NMV F52592); Port Phillip Bay, Area 49 Stn 236 (NMV G1705), Area 5, Stn 169 (NMV G1820), PPBES Stn 966 (NMV F52593); Western Port, Flinders Island (NMV F52594); Shoreham Reef (NMV F52595), CPBS Stn 21N (NMV F52613), CPBS Stn 33S (NMV F52596), Stn WBES 1716-3, WBES 1719-2, WBES 1704-2, WBES 1732-3 (NMV unreg); Wilson's Promontory (NMV F52597-F52598); Gabo Island (AM W200814). New South Wales: Jervis Bay (AM W201158), 20°16'S, 169°51'E, 85-100 m (AM W201532); Port Jackson (AM W201533). Queensland: Moreton Bay (AM W201531); Hervey Bay, Port Vernon (AM W201534); One Tree Island Lagoon (AM W201152); Lizard Island (AM W200728); Thursday Island (AM W201530); Escape Reef 15°50'S, 145°50'E 2(AM W201160). Northern Territory: South West of Nassau River, East Gulf of Carpentaria, 22 m, 16°06'S 140°44'E; Darwin, Vostey Beach (NT W144), Lee Point (NT W147); Port Essington, Table Head (NT W142), (NT W1574); Oxley Island (NT W826).

Description. Alcohol preserved body pale yellow in colour, except for numerous prostomial eye spots arranged in an extensive ring. Prostomium compact with upper lip extended as rectangular forwardly projecting lip. Peristomium with no expansion. Branchiae, 3 pairs, on segments 2, 3 and 4; each branchia with thick main stalk and few short stumpy dichotomous branches. Lateral lobes on segments 2, 3 and 4. Segment 2 with ventrally displaced lateral lobe, narrow elongate lobe just merges onto the ventral pad laterally. Segment 3 with lateral lobe more laterally displaced, small bluntly digitiform and obliquely positioned towards the notopodia (Fig. 5a,b). Segment 4 with small rounded lobe just above the neuropodial tori on following segment. Margins of all the lobes thin, clear markings, perhaps blood vessels can be seen on the margins of the lobes.

Notopodia begin on segment 4, continue for 17 segments, notosetae arranged in 2 tiers, broad-bladed, very narrow-winged capillaries with tips drawn out into fine smooth points. Notosetal blade highly ornamented but margins of setae smooth. Neuropodia begin on segment 5 (setiger 2), continue almost to the pygidium. Thoracic neuropodia fairly compact, glandular tori. Anterior abdominal neuropodia erect rectangular tori, which become progressively shorter towards pygidium. Uncini avicular, short handled (Fig. 5c) with dental formula MF:1:2:3. Posterior thoracic neuropodia with uncini arranged in alternate rows from the seventh uncinigerous segment, with dental formula MF:2:3:2.

Anterior ventral pads form V-shaped central glandular core, but individual pads still recognisable. Posteriorly, ventral pads form midventral glandular thoracic stripe which continues onto the abdomen. Margins of pygidium convoluted to form an anal rosette.

Variation. The paratype material closely resembles the holotype, although some of the branchiae are slightly more branched than those found on the holotype. The markings on the lateral lobes, which may be blood vessels, vary in intensity amongst the type material.

In the non-type material from Shoal Bay, Kangaroo Island, the branchiae and anterior segments are pigmented green. The specimen from Smiths Gulch, Tasmania, lacks eye spots but in all other respects, resembles the type material.

A gravid specimen from Port Lincoln, South Australia (NMV unreg) has a parasitic copepod protruding from the body wall just below the first notopodia. This parasitic copepod closely resembles the one present in *Terebella pappus* (Fig. 22d).

Comments. *Eupolymnia koorangia* n. sp. can be easily distinguished from *E. nebulosa* (Montagu, 1818) with which it has been confused in the past, by the development of lateral lobes. Material of *E. nebulosa* from Southern England, the type locality for the species (BMNH ZK 1948.10.20.107; ZK 1950.6.6.21 and AM W200882), has three pairs of

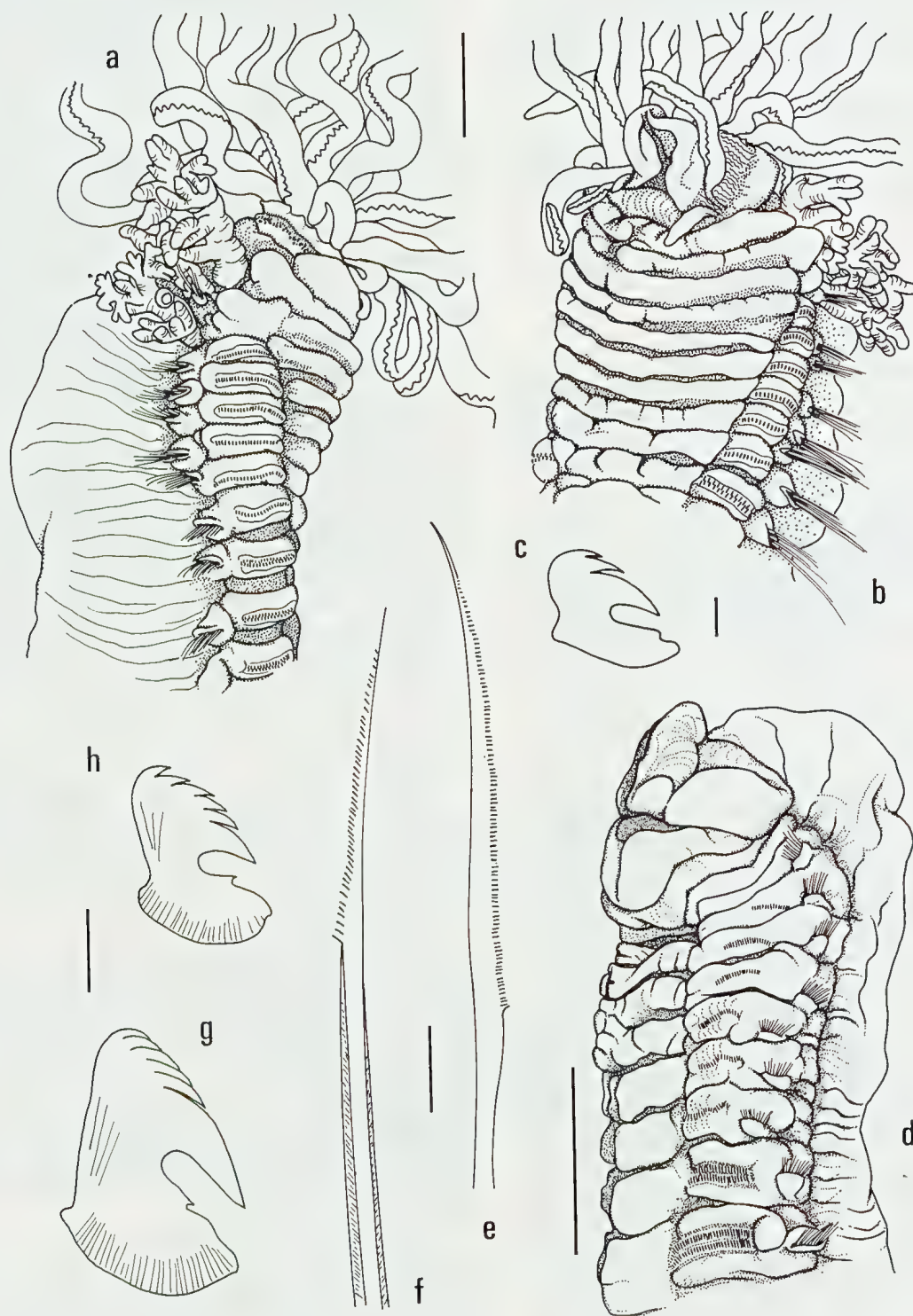


Fig. 5. *Eupolymnia koorangia* n. sp., holotype. a. lateral view of anterior body, scale is 1 mm. b. ventral view of anterior body, scale is 1 mm. c. uncinus from setiger 2 (unciniger 1), scale is 0.01 mm. *Lanassa exelysis* n.sp., holotype. d. lateral view of anterior body, scale is 1 mm. e. notoseta from setiger 9, scale is 0.01 mm. f. notoseta from setiger 9, scale is 0.01 mm. g. uncinus from midbody setiger, scale is 0.01 mm. h. uncinus from posterior body setiger, scale is 0.01 mm.

branchiae, each branchiae with few dichotomous branches and virtually no main stalk. Peristomium expanded as a discrete narrow elongated raised ventral collar. Segment 2 with a small spherical lateral lobe attached to ventral pad to form a bilobed structure. Segment 3 with bilobed spherical lateral lobe, dorsolaterally displaced. Segment 4 with small discrete digitiform lobe which is directed dorsally. This arrangement of lateral lobes differs from that described for *E. koorangia*. We have examined material identified by Knox & Cameron (1971) and Hartmann-Schröder (1979, 1981, 1982, 1984, 1985, 1986) as *E. nebulosa* and all the material agrees with *E. koorangia* n. sp. *Eupolymnia trigonostoma* (Schmarda, 1861), described from off the New South Wales coast, has been referred to *E. congruens* (Marenzeller, 1884) by Hessle, 1917. This species also differs from *E. koorangia* in the development and arrangement of lateral lobes. The type material could not be located and no adequate description is available. Several other species of *Eupolymnia* have been described from areas outside Australasia. Most of these species are poorly described, with no detailed descriptions of the shape and orientation of the lateral lobes. We believe that the shape, orientation and development of lateral lobes in *Eupolymnia* are important specific characters. A revision of the genus is needed.

Etymology. The specific name refers to an Aboriginal name for kangaroo, the type locality for the species (Kangaroo Island in South Australia).

Habitat. Found intertidally to depths of 85–100 m, often associated with seagrass beds in shallower depths.

Distribution. Widespread around Australia, locally can be abundant.

Hadrachaeta Hutchings

Hadrachaeta Hutchings, 1977: 16.

Prostomium compact with thickened outfolded lips, numerous thick grooved buccal tentacles. Branchiae, 3 pairs on segments 2–4, consisting of simple filaments. Lateral lobes poorly defined. Notopodia from segment 4 (3rd branchiferous) and continue for 16 segments; notosetae finely serrated capillaries. Uncini from segment 5 (setiger 2) and present on all following segments to pygidium. Uncini of first 4 rows heavily chitinated long handled hooks, following ones avicular, and arranged in double rows on posterior thorax.

Type-species. *Hadrachaeta aspeta* Hutchings, 1977, by original designation.

Hadrachaeta aspeta Hutchings

Hadrachaeta aspeta Hutchings, 1977: 17, fig. 8a–d.—Hutchings & Murray, 1984: 96–97.

Comments. Extensive collecting on intertidal mud flats on the seaward side of mangroves along the east and northern coast of Australia has confirmed its limited geographical distribution and restricted habitat, intertidal mudflats in front of *Avicennia* mangroves. This genus is monospecific.

Distribution. New South Wales (Hawkesbury River, Broken Bay), Queensland (Moreton Bay).

Lanassa Malmgren

Lanassa Malmgren, 1866: 385–386.

Laphaniella Malm, 1874: 98.

Pherea Saint-Joseph, 1894: 167.

Branchiae absent. Lateral lobes sometimes present; glandular pads well developed. Thoracic notopodia begin on segment 4 and continue for 15 segments. Notosetae serrated capillaries. Neuropodia from segment 5 (setiger 2), with avicular uncini arranged in double rows on some segments.

Type species. *L. nordenskioldi* Malmgren, 1866, by original designation.

Comments. The genus *Lanassa* has not previously been recorded from Australia. Eight species of the genus have been described worldwide, mainly from cold and deep water. Several of the species have not been reported since they were originally described.

Type material of *Lanassa benthaliana* McIntosh, 1885 (BMNH 1885.12.1.357) has been examined. It is poorly preserved, in two fragments and is probably indeterminable unless additional material can be found. Similarly the type of *L. sarsi* McIntosh, 1885 (BMNH 1885.12.1.356) is in fragments which are not consecutive and again this species is probably indeterminable unless additional material from the type locality can be collected. Currently, neither of these species can be adequately defined because of McIntosh's incomplete descriptions and the poor state of the respective type material. The holotype of *L. capensis* Day, 1955 (BMNH 1961.16.90) appears to have branchial scars which would place it in another genus. Four other species of *Lanassa* and one subspecies have been described according to Hartman (1959, 1965). These are all found in cold waters in the northern hemisphere. The original descriptions of *L. nordenskioldi* Malmgren, 1866, *L. praecox* (Saint-Joseph, 1899), *L. venusta* (Malm, 1874), *L. venusta pacifica* Annenkova, 1938 and *L. gracilis* (Moore, 1923) are inadequate regarding the structure of notosetae in the notopodia along the thorax and the segments on which the uncini are arranged in single and double rows. Thus the genus is in need of revision. A full description of the type species *L. nordenskioldi* Malmgren, 1866, is required before any such revision is attempted.

Key to the Australian species of *Lanassa*

1. Eye spots present; prostomium compact; uncini arranged in double rows for 5 segments beyond last pair of notopodia. *L. ocellata*
- Eye spots absent; prostomium with a tongue-like projection; uncini arranged in double rows for 3 segments beyond last pair of notopodia. *L. exelysis*

Lanassa exelysis n. sp.

Fig. 5d–h

Material examined. HOLOTYPE: Victoria: Swan Bay, Port Phillip Bay, 38°14'S, 144°39'E (AM W200603) subtidal, fine sand silt, complete individual 20 mm in length and 1.5 mm in width with approximately 55 setigers. PARATYPES: All from same locality as holotype, (NMV F52565), (AHF Poly 1467), (USNM 99968), (BMNH ZB 1986.64), (AM W200604) all posteriorly incomplete, ranging in length from 12–20 mm and 1.5 mm in width.

Additional material examined. Victoria: Port Phillip Bay Stn 953, 38°09'03"S, 144°27'07"E, sand, 3 m (AM W16122).

Description. Preserved animal colourless. Extreme posterior end is regenerating, consists of 10–15 very compact, condensed segments. Prostomium with no buccal tentacles remaining. Prostomium extended forwards ventrally as tongue-like projection, with lateral expansions, anterior margins thickened, glandular. Peristomial collar extends posteriorly in U-shaped backwardly pointing tongue, covers first ventral glandular pad (Fig. 5d). Eye spots absent. Lateral lobes absent.

Distinct ventral glandular pads, initially well developed and segmentally distinct, for first 8 setigers, then pads rapidly taper into narrow ventral stripe which continues to pygidium. Notopodia begin on segment 4, continues for 15 segments. Notopodia well-developed elongate rounded podia with small patch of pigment on either side of emergent setae. Between the notopodia, white elongate segmental lateral glandular patches are present. Neuropodia begin on segment 5 (setiger 2) and continue to within 1 or 2 segments of pygidium. Thoracic neuropodia slightly raised glandular. Abdominal neuropodia more erect than thoracic ones, mounted on glandular tori.

Anterior notosetae, narrow-winged capillaries with long pointed tips, margins of blade faintly hispid; within bundle of setae, 2 groups of setae present one short, other long. In posterior segments in addition to those setae occurring anteriorly, narrow bladed, capillary setae with denticulate margins occur (Fig. 5e,f). Intermediate setae between these 2 types of setae also occur. Difficult to ascertain exactly where denticulate setae first occur, but about segment 12 (setiger 8).

Neuropodia with avicular uncini (Fig. 5g,h) initially arranged in single rows, then in double rows, face to face on setiger 11–21 (setiger 8 to 3 segments beyond the last notosetigerous segment). Subsequently uncini arranged in single rows,

gradually length of neuropodial tori becomes very short, with few uncini present in each torus.

Neurosetae with the following dental formula MF:3-5:6:8-11:α:α. Body cavity with no gametes visible. Nephridial papillae absent.

Variation. Some of the paratypes have visible female gametes in the body cavity, i.e. coelomic gametes, but no nephridial papillae present. Buccal tentacles short and grooved.

Comments. *Lanassa exelysis* n. sp. differs from the other Australian species of the genus, *L. ocellata* n. sp., in the shape of the prostomium which is more elongate, and has eye spots which are absent in *L. exelysis*. However the major differences are in the type of the posterior notosetae which are broad bladed in *L. ocellata*, and narrow bladed in *L. exelysis*, and the segments on which the uncini are arranged in double rows, 11–21 in *L. exelysis* and 11–23 in *L. ocellata*. These differences are specific differences rather than ones related to size.

For a discussion on other species currently assigned to the genus *Lanassa* see comments given after the generic diagnosis.

Etymology. The specific name *exelysis* is greek (f) and refers to the mouth of the estuary, where this species occurs.

Habitat. Found subtidally in fine sand and silt in protected marine embayments.

Distribution. Victoria (Swan Bay, Port Phillip Bay).

Lanassa ocellata n. sp.

Fig. 6a–d

Material examined. HOLOTYPE: New South Wales: Murumbulaga Point, Twofold Bay 37°06'S, 149°56'E, intertidal, rock platform, cryptic fauna (AM W200602), 4 mm long and 1.0 mm wide, posteriorly incomplete.

Description. Preserved specimen colourless. Prostomium compact with few thickened buccal tentacles arising from thickened margin which forms small rounded tongue-like extension ventrally. Small discrete group of eye spots present laterally. Branchiae completely absent. Lateral lobes absent. Well developed ventral discrete segmental glandular pads present on segments 4–16 (setigers 1–13), then size of pads decreases, tapers to narrow ventral stripe which continues along rest of body (Fig. 6a).

Notopodia begin on segment 4, continue for 15 segments, well-developed elongate podia. Notosetae anteriorly, of 1 type, narrow-winged capillaries with faintly hispid tips (Fig. 6b); notopodia of midbody

segments, with additional type of notosetae present, these are short, broad-bladed setae with denticulate margin (Fig. 6c). In posterior setigers at least 3–4 of these denticulate setae are present per notopodial fascicle. Denticulate setae are present in at least the last 8 pairs of notopodial fascicles (setigers 8–15); bundles of notosetae from anterior notopodia often include large numbers of damaged setae, so the exact setiger on which the denticulate setae first occur cannot be stated. Neuropodia from segment 5 (setiger 2) occur on all subsequent segments present on the holotype. Thoracic neuropodia well developed, glandular. Abdominal neuropodia glandular, raised, forming 2 discrete ridges along either side of narrow ventral stripe. Uncini avicular (Fig. 6d) with strongly crested head, initially arranged in single rows, from segment 11–23 (setiger 8 to 5 segments beyond the last notosetigerous segment), arranged in double rows face to face; for remaining 3 neuropodial segments uncini arranged again in single rows. Dental formula of uncini as follows MF:5-7:6-8: α : α .

Nephridial papillae absent. Groups of spermatogonia in form of rosettes (coelomic gametes) are present in body cavity.

Comments. For comments on the differences between *Lanassa ocellata* n. sp. and *L. exelysis* n. sp. see the description of *L. exelysis*.

Etymology. The specific name refers to the presence of eye spots.

Habitat. Found as crevice fauna living intertidally on rocky shores.

Distribution. New South Wales (Twofold Bay).

Lanice Malmgren

Lanice Malmgren, 1866: 379.

Venusia Johnston, 1865: 241.

Wartelia Giard, 1878: 1147.

Prostomium compact. Branchiae, 3 pairs present on segments 2, 3 and 4, branchiae branched. Lateral lobes present on peristomium and segment 3. Notopodia present from segment 4, 17 pairs, notosetae smooth-tipped capillaries. Neuropodia from segment 5 (setiger 2), initially uncini arranged in single rows, subsequently arranged back to back in posterior thorax. Neurosetae avicular uncini. Tube with or without branched fine-meshed fan attached to opening.

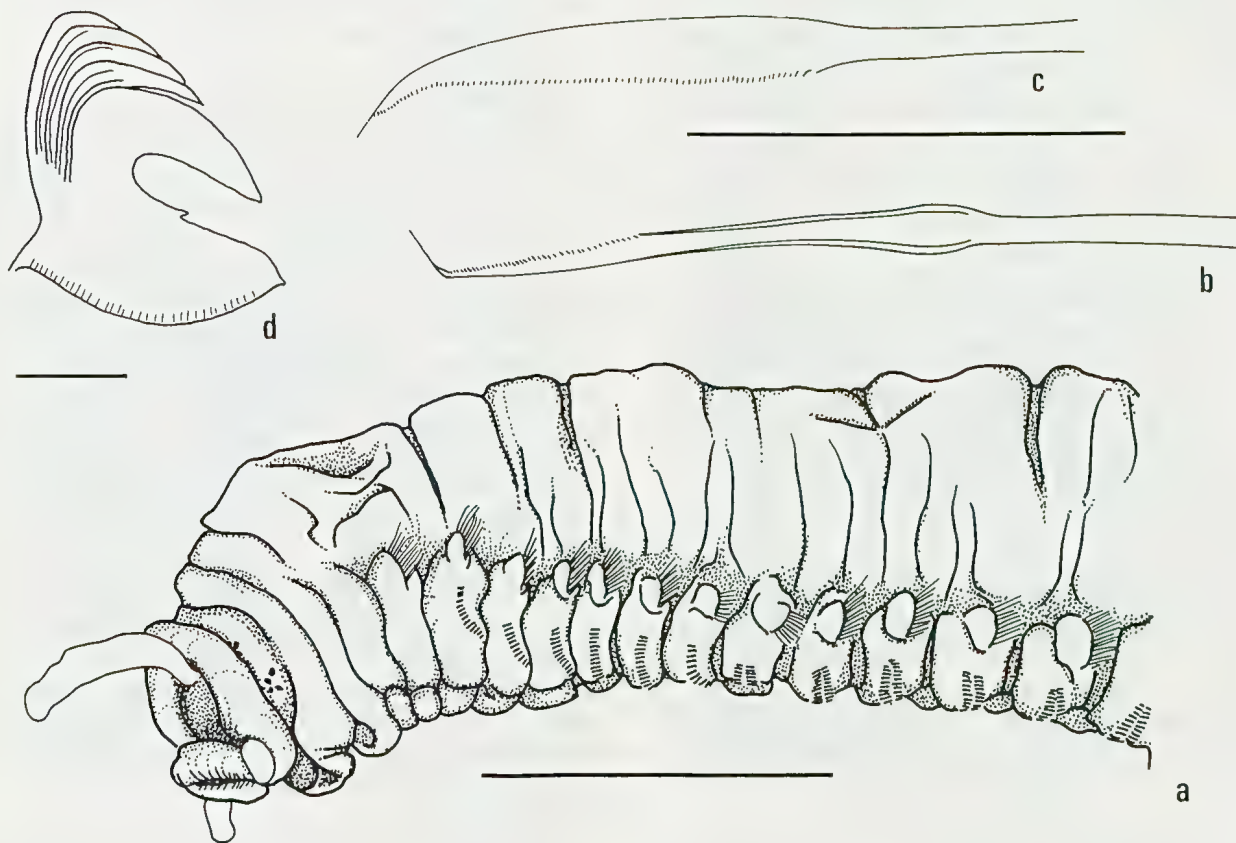


Fig. 6. *Lanassa ocellata* n. sp., holotype. a. lateral view of anterior body, scale is 1 mm. b. notoseta from anterior body setiger, scale is 0.1 mm. c. notosetae from posterior body setiger, scale is 0.1 mm. d. uncinus from midbody setiger, scale is 0.01 mm.

Type species. *Nereis conchilega* Pallas, 1766, by monotypy.

Comments. We have expanded the definition of the genus to clearly state which segments lateral lobes occur on, and have indicated that the opening of the tube may be smooth or ornamented.

***Lanice bidewa* n. sp.**

Fig. 7a–c

Lanice conchilega.—Augener, 1927: 251.—Knox & Cameron, 1971: 38.—Hutchings, 1977:17–18.—Hartmann-Schröder, 1982: 90. *Non* Pallas, 1766.

Material examined. HOLOTYPE: Victoria: Cape Everard, 37°16'S, 150°03'E (AM W200764) 10 m in holdfasts of the algae *Phyllospora*, posteriorly incomplete, 2 cm in length and 2 mm maximum width with 12 abdominal segments. PARATYPES: Victoria: Cape Everard, 4(USNM 99969), 4(BMNH ZB 1986.65–67). New South Wales: Green Point, Port Jackson 33°53'S, 151°13'E (AM W200687), 1(AHF Poly 1468). All paratype material posteriorly incomplete.

Additional material examined. Western Australia: North West Shelf. Stn 01-83-B4G, 19°05.2'S, 118°54.1'E (AM W200832), Stn 04-83-B3G, 19°55.5'S, 117°56.1'E (AM W200833), Stn 03-83-B8GR9, 19°29.6'S, 118°52.2'E (AM W200835); Cable Beach, Broome 1(NT W2491), 1(HZM P16618); North West Cape, Neds Beach (WAM 371); Shark Bay, outer bar, north-west of Monkey Rock, (WAM 53-84); Dampier Archipelago, Kendrew Island (WAM 28-84). South Australia: Kangaroo Island, Penneshaw Jetty (AM W200829). Bass Strait: Stn 107, 109, 112, 115, 117, 120, 121, 128, 130, 131, 139, 156, 161, 169, 190, 199, 204 and 205 (NMV unreg). Victoria: Port Phillip Bay (NMV G1731); Western Port, Stn 10 (NMV unreg); Gabo Island (AM W200816), (AM W200818). Queensland: Moreton Bay (AM W5101), (AM W7088); Lizard Island (AM W200871), (AM W200870).

Description. Alcohol preserved animal colourless, lives in tube composed of sand and shell fragments, smooth margins to opening of tube. Prostomium compact, with eye spots present. Numerous grooved buccal tentacles present. Prostomium with anteriorly projecting U-shaped lip. Peristomium with large oval-shaped lobes encompassing base of buccal tentacles, lobes connected midventrally by thinner V-shaped connecting strip. Segment 2 lacks lateral lobes. Segment 3 with smaller laterally displaced, rectangular-shaped lateral lobe, not as glandular as peristomial lobes, margins of lobes on segment 3 convoluted. Segment 4 without lateral lobes (Fig. 7a,b).

Branchiae, 3 pairs, on segments 2, 3 and 4, with short main stalk, dichotomous branching, individual branches thick, short. All pairs of branchiae equal in size.

Notopodia from segment 4, continue for 17 segments. Notosetae consist of 2 tiers of broad bladed, narrow-winged capillaries with long, fine, smooth tips. Neuropodia from segment 5 (setiger 2), occur on all following abdominal segments present.

Uncini initially arranged in single rows, but from seventh uncinigerous thoracic segment to last thoracic segment, uncini arranged in double rows back to back. Uncini arranged in single rows on abdominal segments. Uncini short handled, avicular (Fig. 7c) with dental formula ranging from MF:2:1 to MF:3:2. Uncini arranged on long neuropodial tori, in thorax but tori not markedly glandular. Abdominal tori are rectangular, erect, glandular structures.

Ventral pads, first 5 distinct, then followed by very weakly segmented glandular area, forming central solid ventral core, gradually narrows to form narrow midventral glandular groove.

Nephridial papillae present on setigers 3–6, present just posterior to notopodia. Holotype not gravid.

Variation. The paratypes exhibited some variation in dentition of the uncini in comparison to the holotype, from MF:2:2 to MF:3:3.

Comments. All the material examined (only a portion is listed in the Material examined) is small, although some of it is gravid. The material from North West Shelf is particularly small and not well preserved. All specimens still associated with tubes have tubes with smooth margins. All previously described species of *Lanice* have tubes with frayed margins. Within the Australian Museum collections there are tubes with frayed margins characteristic of *Lanice* but these tubes are all empty. This may mean that another species of *Lanice* is present in Australian waters.

According to Day & Hutchings (1979), only two species of *Lanice* have been recorded from Australia, *L. conchilega* (Pallas, 1766) and *L. flabellum* Baird, 1865. Material labelled as *Terebella flabellum* juvenile? collected by J.B. Jukes in 1846 from 'Australia' and lodged in the British Museum (Natural History), consists of two empty tubes. This may be the material described by Baird. Similarly, New Zealand records appear to consist only of tubes of this species. Material labelled as *Lanice flabellum* (BMNH ZB 1928.2.29.350) collected by the "Terra Nova" expedition in 1910, from off Three Kings Island, New Zealand, consists only of tubes with a fan-shaped structure attached to the opening of the tube. Hartman (1959) suggested that *L. flabellum* was indeterminate as only tubes were present. However some tubes labelled as *L. flabellum* present in the British Museum (Natural History) collections from the Antarctic do contain specimens, and these will be described in a paper on Antarctic terebellids currently being prepared by Hutchings. So at this stage it is unknown if *L. flabellum* occurs in Australian waters. All the Australian records of *L. conchilega* have been examined by us and are referred to *L. bidewa* n. sp.

Lanice conchilega has been described from around the world. In most cases the descriptions are inadequate to define the species. Type material of *L. conchilega* has not been located and we suspect it does not exist. Material from the type locality, which is

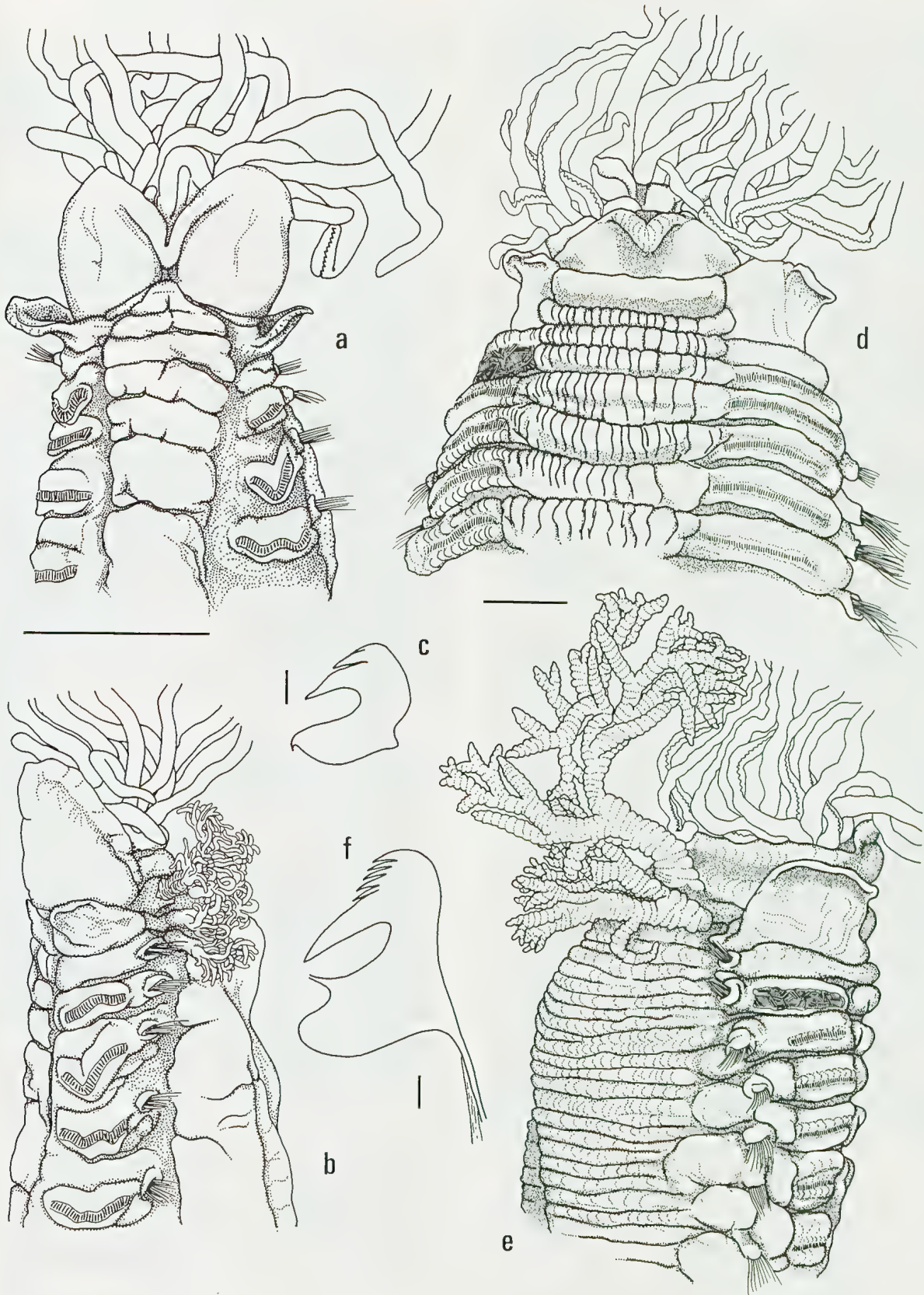


Fig. 7. *Lanice bidewa* n. sp., holotype. **a.** ventral view of anterior body, scale is 1 mm. **b.** lateral view of anterior body, scale is 1 mm. **c.** uncinus from midthoracic setiger, scale is 0.01 mm. *Lanicides fascia* n. sp., holotype. **d.** ventral view of anterior body, scale is 1 mm. **e.** lateral view of anterior body, scale is 1 mm. **f.** uncinus from uncinger 1, scale is 0.01 mm.

given as Holland by Hartman, 1959 has been examined (USNM 44397, washed ashore at Katwyk, Netherlands). This species differs from *L. bidewa* n. sp. in the structure of the branchiae and the lateral lobes. The branchiae in *L. conchilega* consists of many fine branches produced by extensive dichotomous branching. The lateral lobe in *L. conchilega* on segment 3, is a narrow rectangular lobe with a dorsolateral flag-like extension. The peristomium has a well-developed lateral lobe which continues dorsally as a narrow shelf; such a shelf is absent in *L. bidewa*. The prostomium of *L. conchilega* has a U-shaped bifid lateral lip which is corrugated unlike the simple U-shaped lip found in *L. bidewa*. The two species also differ in the arrangement and development of glandular tissue on the ventral pads and around the notopodia. In *L. conchilega* the area around the notopodia is very glandular forming a markedly corrugated glandular lateral stripe along the length of the thorax. In *L. conchilega* the ventral pads of segments 2, 3 and 4 are fused to form a slightly globular ventral pad, whereas in *L. bidewa* the ventral pads of these segments are distinct. Nephridial pores present on segments 4 to 10 on *L. conchilega* and on segments 6 to 9 in *L. bidewa*. Another specimen of *L. conchilega* from the Bay of Naples (USNM 5112) closely resembles USNM 44397. Neither lots of *L. conchilega* include any tubes.

All preserved material of *L. bidewa* is small and colourless whereas *L. conchilega* regularly reaches 25 to 30 cm in length and the body can be rose, yellow or brown, according to Fauvel (1927), although it is unclear if Fauvel is referring to live or preserved material. *Lanice bidewa* is a cryptic species, living in coral substrates, in algal holdfasts or sabellariid reefs, whereas *L. conchilega* occurs in dense colonies on sandy beaches.

The few other species of *Lanice* described are typically deep water species, whereas *L. bidewa* occurs over a wide depth range.

Etymology. The specific name *bidewa* refers to the name of the aboriginal tribe living in the region of Cape Everard, the type locality of this species.

Habitat. Found in algal holdfasts, sabellariid reefs or living as a cryptic species in coral substrates, intertidally to depths of 120 m.

Distribution. Western Australia, South Australia, Victoria, New South Wales, Queensland.

Lanicides Hessle, emended.

Lanicides Hessle, 1917: 165.—Fauchald, 1977: 131.

Branchiae, 2 or 3 pairs on segments 2, 3 and 4, branchiae branched. Lateral lobes present on segment 3, sometimes on peristomium. Notopodia from segment 4, notosetae smooth tipped, some setae with serrated margins; long shafted uncini present from segment 5 (setiger 2); subsequently uncini become short handled avicular uncini. Uncini initially arranged in single rows, but on posterior thoracic segments uncini arranged in double rows face to face, abdominal uncini arranged in single rows.

Type species. *Terebella* (*Phyzelia*) *bilobata* Grube, 1877, designated by Hessle, 1917.

Comments. We have emended the generic diagnosis of *Lanicides* as currently defined, to include species with two or three pairs of branchiae and species with lateral lobes developed on the peristomium. Species possessing this arrangement of lateral lobes, cannot be placed in the genus *Pista* as they lack lateral lobes on segments 2 and 4, a generic character of *Pista*. However we suspect that a detailed examination of all species currently assigned to these genera would necessitate considerable reassignment within these genera. Many of the original descriptions do not clearly state the positioning of the lateral lobes or give details on other characters which would clarify their generic status.

We have in this paper described three new species of *Lanicides*, including *L. lacuna*, with 19 to 20 pairs of notopodia. All previously described species of *Lanicides* have 17 pairs of notopodia. Until a revision of the complex of genera containing long handled uncini, with smooth tipped notosetae (*Betapista*, *Eupistella*, *Lanicides*, *Opisthopista*, *Pista*) is carried out, it seems appropriate to retain *L. lacuna* n. sp. in the genus *Lanicides*. The shape of the uncini and arrangement of lateral lobes, places it within the currently accepted generic diagnosis of *Lanicides*. The generic diagnosis has also been emended to include the presence of some finely serrated notosetae (Fig. 9).

The genus *Lanicides* has not previously been described from Australia.

Key to the Australian species of *Lanicides*

1. 3 pairs of branchiae. *L. tribranchiata*
- 2 pairs of branchiae 2
2. 17 pairs of notopodia; lateral lobe on segment 3 rectangular. *L. fascia*
- 19–20 pairs of notopodia; lateral lobe on segment 3 narrow and elongate. *L. lacuna*

Lanicides fascia n. sp.

Fig. 7d–f

Nicolea bilobata.—Augener, 1914: 92. *Non* Grube, 1877.*Nicolea venustula*.—Hartmann-Schröder, 1979: 148 (in part, rest = *Pista violacea*); 1980: 77. *Non* Montagu, 1818.*Lanice conchilega*.—Hartmann-Schröder, 1979: 147. *Non* Pallas, 1766.

Material examined. HOLOTYPE: South Australia: West side of Cape Northumberland, Port Macdonnell 38°03'S, 140°42'E (AM W200608), under rocks in sheltered pool, complete individual, 4.5 cm in length, 5 mm maximum width. PARATYPES: South Australia: Speeds Point, Streaky Bay 32°48'S, 134°13'E (BMNH ZB 1986.68) complete, 2 cm in length and 2 mm maximum width; Sellicks Beach 35°20'S, 138°27'E, 1(USNM 99970) posteriorly incomplete, 3 cm in length and 4 mm maximum width; Kangaroo Island, Stokes Bay, 35°37'S, 137°12'E, 1(AHF Poly 1469) complete, 2.5 cm in length and 2 mm maximum width. Victoria: Western Port, 38°14.47'S, 145°21.86'E 3(NMV F52566, F52567, F52568), complete, all about 5 cm in length with maximum width, at midthorax of 4 mm.

Additional material examined. Western Australia: Broome (HZM P16619, P16685); Exmouth (HZM P16622); Koombana (HZM V8265); Rottnest Island, North Point (WAM 62-74). South Australia: Kangaroo Island, Stokes Bay (AM W200696), Emu Bay (AM W200697); Cape Robe, Karatta Beach (AM W200695), West side of Cape Northumberland, Point McDonnell (AM W200701). Tasmania: Boat Harbour, Western Bay (TASM K1021). Victoria: Port Phillip Bay, Phillip Island (NMV unreg); Near Eagles Nest (NMV unreg). New South Wales: Twofold Bay (AM W200688); Bass Point (AM W200694); Sydney, North Head (AM W200691). Queensland: Caloundra (AM W200689).

Description. Lives in tube made of cemented shell fragments, firmly cemented onto coralline algae.

Preserved animal, pale pink in colour, with numerous buccal tentacles. Prostomium compact. Eye spots absent. Peristomium extended forwards on the ventrum to form slightly tripartite glandular structure.

Branchiae, 2 pairs, on segments 2 and 3, first pair the largest. All branches, main stem of branchia ringed transversely, dichotomous branching but each branchia with relatively few branches. First pair of branchiae dorsally displaced in comparison to second pair of branchiae.

Lateral lobes present on segment 3, rectangular, with margins thinner than base, appearing slightly convoluted; longitudinal markings on surface of lobe. Segment 4 with slightly thickened anterior margin, but not forming lateral lobe (Fig. 7d,e).

Ventral glandular pads initially fairly discrete, well demarcated segmentally, disappear by about setiger 13.

Notopodia begin on segment 4, continue for 17 segments; podia small globular structures with notosetae emerging from sheath in middle of podia. Setae within fascicle tapered, longest setae nearest

dorsum. Notoetae, consist of 2 tiers of broad-bladed, narrow-winged capillaries, with very weakly serrated tips. Neuropodia begin on segment 5 (setiger 2), continue to pygidium. Thoracic neuropodia consist of very long rows of uncini, abdominal tori very glandular, with uncinal rows deeply embedded in the tori. Abdominal uncini arranged in a slightly curved shaped row; abdominal tori rectangular lying flat against the body wall. Uncini avicular (Fig. 7f), with a short shaft present only on first uncinigerous segment, absent on all subsequent uncinigerous segments. Uncinal shaft easily damaged or broken while preparing uncinal mount. Uncini initially arranged in single rows, then from seventh uncinigerous segment to last thoracic segment, uncini arranged in double rows face to face. Abdominal uncini arranged in single rows. Uncini of first thoracic uncinigerous segment with strongly crested head having a dental formula of MF:6:6-8:α.

Nephridial papillae present on segments 3 and 4, situated just posteriorly to second pair of branchiae and first notopodia respectively. Coelomic gametes absent. Anus small muscular sphincter with margins of opening ornamented with numerous very fine papillae.

Variation. The paratypes have faint brown pigment along the sides of the grooved buccal tentacles. One of the paratypes exhibits very prominent blood vessels running through the branchiae. None of the type material is gravid.

Comments. *Lanicides fascia* can be distinguished from *L. taboguillae* (Chamberlin, 1919) by the arrangement of lobes on segment 3, and the development of the peristomium, and by the limited development of teeth above the main fang of the uncini. *Lanicides vayssierei* (Gravier, 1911) has been synonymised with *L. bilobata* (Grube, 1877) (see Hartman, 1966b for full synonymy) and can be distinguished from *L. fascia* by the presence of two pairs of lateral lobes on segments 2 and 3. Material identified by Augener, 1914 as *Nicolea bilobata* (Grube, 1877), has been examined (HZM V8265), and is referred to *Lanicides fascia*. Hessle (1917) had already transferred Augener's record to the genus *Lanicides* and synonymised it with *L. vayssierei* (Gravier). However Augener's material has lateral lobes only on segment 3 and can thus be distinguished from *L. vayssierei*. *Lanicides vayssierei* was originally described from the Straits of Magellan a very different habitat from Augener's collecting site of Koombana in Western Australia.

Some of the material described by Hartmann-Schröder as *Nicolea venustula* was incorrectly identified and has been referred to *Lanicides fascia*.

Etymology. The specific name, *fascia*, is latin for band, stripe or girdle which refers to the banded stalk of the branchiae.

Habitat. Found from intertidal to shallow subtidal depths, where firm substrate is available for the tube to be attached to.

Distribution. Western Australia (Broome, Exmouth, Koombana, Rottnest Island), South Australia (widespread), Tasmania, Victoria (Port Phillip Bay, Western Port), New South Wales (Twofold Bay, Bass Point, off Sydney), Queensland (Caloundra).

Lanicides lacuna n. sp.

Figs 8a–d; 9a–c

Material examined. HOLOTYPE: Queensland: Great Barrier Reef, One Tree Island 23°30'S, 152°05'E (AM W200609), dead coral substrate in lagoon, 10 m, in 2 fragments, anterior end 2 cm in length, 3 mm maximum width, posterior fragment 3.5 cm in length. PARATYPES: 1(USNM 99971), 1(BMNH ZB 1986.69), 1(AM W200610), 1(AM W200611). All paratypes from same habitat as holotype. PARATYPES: USNM, posteriorly incomplete, 2 cm in length, 2.5 mm maximum width, thorax and 18 abdominal segments; BMNH, complete 4 cm in length, 2.5 mm maximum width; AM, both specimens posteriorly incomplete.

Additional material examined. Queensland: One Tree Lagoon, 10 m, 1(AM W200756), 1(AM W200757), 1(AM W200758), 1(AM W200759).

Description. Preserved specimen, pale yellow with some dark brown pigment on buccal tentacles. Prostomium compact, eye spots absent. Branchiae, 2 pairs, on segments 2 and 3, first pair largest. Each branchia dichotomously branches almost as soon as main stalk emerges from body wall; several dichotomous branches per branchia.

Peristomium with ventrally arranged glandular, lateral lappets connected mid-dorsally, margins of lappet slightly convoluted (Fig. 8a,b). Segment 2 with no lateral lobes, segment 3 with elongate narrow rectangular lobe. Segment 4, without discrete lateral lobes but entire neuropodia enlarged, glandular. Notopodia from segment 4, continue for 19 segments, notopodia small, globular. Notosetae, narrow-winged, broad-bladed capillaries, surface of blades with faint surface striations, weakly denticulate margins (Fig. 9a–c). Notosetae within fascicle graded in length.

Neuropodia from segment 5 (setiger 2), uncini initially arranged in single rows, from seventh uncinigerous segment to end of thorax, uncini arranged in double rows, face to face, arranged in single rows on abdomen. Uncini avicular with well-developed chitinised shaft, however shaft can easily be broken off during preparation of uncinal mount, in which case point of attachment of shaft to base of uncini is easily recognisable as damaged surface (Fig. 8c). Dental formula of thoracic uncini MF:3:6:7:6:7:α. Uncinal shaft well developed on following 2 uncinigerous segments, however by uncinigerous segment 4, shaft is markedly smaller, reduction continues over next few segments until shaft completely disappears.

Thoracic uncini arranged in very long rows, abdominal uncini arranged on short sessile podia arranged on very glandular area of body wall.

Glandular areas form 2 lateral glandular ridges running along length of abdomen (Fig. 8d). Ventral pads very poorly defined, entire ventrum, lateral areas of thorax, all fairly glandular. Tendency for glandular pads on which neuropodial tori occur to continue across ventrum, thus connecting right and left hand side of body. Glandular area above thoracic tori extending dorsally above notopodium in tongue-like projection, very glandular with speckled brown pigment (Fig. 8a). Pygidium small opening, surrounded by tight sphincter muscle. Nephridial papillae situated very slightly dorsally and posteriorly below point of insertion of notopodia, on segments 4–8 (setigers 1–5). No gametes visible within body cavity.

Variation. The paratypes exhibit some variation in the intensity of pigmentation of the glandular area above the notopodia, and the extent to which this pigmented glandular area extends onto the abdomen. The paratype (USNM 99971) has 20 pairs of notopodia.

Comments. *Lanicides lacuna* n. sp. can be distinguished from the other previously described species of *Lanicides* by having 19 to 20 pairs of notopodia instead of the typical 17 pairs.

Etymology. The specific name *lacuna* refers to the habitat in which this species lives, and is the latin word for a pool or pond.

Habitat. Found in dead coral substrate in One Tree Island lagoon, at 10 m.

Distribution. Queensland (One Tree Island, Great Barrier Reef).

Lanicides tribranchiata n. sp.

Fig. 8e–i; 9d–f

Material examined. HOLOTYPE: New South Wales: west side of Solitary Island, 30°12'S, 153°16'E, 12 m (AM W200605), 2.5 cm in length and maximum width 5 mm. PARATYPES: Western Australia, approximately 18 km north of Dongara 29°07'S, 114°50'E, 2(WAM 39-84 series), pipe dredge, MV 'Sprightly' Dredging Cruise 1976; Bass Strait, Stn 212, 38°15'S, 147°22'E, 16 m 3(NMV F52569, F52570, F52571), posteriorly incomplete. Victoria: Cape Wellington, Wilson's Promontory north-east shore 38°56'S, 146°22'E, 1(NMV F52572) posteriorly incomplete. New South Wales: reef off Avalon 33°38'S, 151°20'E, 40 m 1(USNM 99972); Coffs Harbour, 30°18'S, 153°09'E, 1(BMNH ZB 1986.70), 1(AM W200607) on old wharf pilings, tubes cemented between barnacle clumps, 3–6 m; South West Solitary Island, west side 1(AM W200608).

Paratype material posteriorly incomplete, range of maximum anterior width varying from 3–4 mm, (AM W200607-8), complete individuals 3 cm length and maximum thoracic width 4.5 mm.

Additional material examined. Western Australia: 18 km north of Dongara. MV. 'Sprightly' dredging cruise 29°07'S, 114°50'E, 18.3 m (WAM 39-84). New South Wales: Port Hacking, Ship Rock, rock face, 20 m 1(AM W200684).



Fig. 8. *Lanicides lacuna* n. sp., holotype. **a.** lateral view, anterior body, scale is 1 mm. **b.** ventral view anterior body, scale is 1 mm. **c.** uncinus from setiger 2 (first uncinigerous row), scale is 0.1 mm. **d.** ventral view, posterior body, scale is 1 mm. *Lanicides tribranchiata* n. sp., holotype. **e.** lateral view, anterior body, scale is 1 mm. **f.** ventral view, anterior body, scale is 1 mm. **g–h.** uncinus of setiger 2 lateral and frontal views, scale is 0.1 mm. **i.** uncinus from posterior thoracic setiger, scale is 0.1 mm.

Description. Complete specimen, coiled, body strongly tapered, very thin posterior abdomen. Preserved body, pale yellow, buccal tentacles banded with pale purple. Prostomium compact, with ventral lip extended forwards to form small tongue with thickened glandular margin. Eye spots absent.

Branchiae, 3 pairs on segments 2, 3 and 4, first pair largest; each branchia with thickened main stalk, then with numerous short, equal, dichotomous branches. Lateral lobes present on peristomium. Lobe displaced ventrally, rectangular in shape, with thinner anterior margins which are slightly convoluted, 2 lobes meet midventrally.

Segment 3 has large semi-circular lateral lobe, with thickened base, thinner, less glandular margins which results in convoluted appearance to margins of the lobe. Lobe displaced laterally in comparison to those present on peristomium. Segment 4 has thickened ridge to anterior margin of segment, but no discrete lobe (Fig. 8e,f).

Ventral pads, initially on anterior thorax, well demarcated, individual pads with narrow vertical banding; by about setiger 10, pads decrease in width, by end of thorax, pads no longer present. Midventral groove continues along part of abdomen.

Notopodia begin on segment 4, continue for 17 setigers; podia small squat structures embedded in glandular issue. Notoetae, consist of broad-bladed, narrow-winged capillaries, with smooth tips, blades with vertical striations, setae arranged in 2 tiers, with some variation in length of setae within tier. Some setae with faintly serrated tips (Fig. 9d-f). Neuropodia begin on segment 5 (setiger 2), and continue to pygidium. Thoracic neuropodia very glandular, abdominal uncini arranged on rectangular erect podia, size of tori decreases posteriorly. Uncini are initially arranged in single rows, from seventh uncinigerous segment, uncini arranged in double rows, face to face. Uncini are arranged in single rows again from beginning of abdomen. Uncini avicular, initially with well-developed chitinous shaft (Fig. 8g,h) but by uncinigerous segment 5, shaft no longer present (Fig. 8i). Dental formula MF:2:1:4 (Fig. 8h). Shaft and margins of uncini easily damaged whilst preparing uncinal mount however, when this happens, torn surface is easily visible at base of uncini where shaft has been broken off. Anterior uncini with well-developed tongue on button of uncini which is easily broken off during preparation of uncinal mounts; appears that tendon is attached to tongue. Pygidium narrow smooth ring. No coelomic gametes visible within body cavity. Nephridial papillae not seen.

Variation. The paratype material which comes from a variety of locations exhibits the following variation; the presence of banded buccal tentacles in some specimens, whereas in others tentacles appear colourless. It is unclear whether this is a result of the fixation method used or a variable character. Similarly the Western Australian material exhibits

fragments of golden brown pigmentation adjacent to the ventral pads at the margin of the neuropodial tori, such pigmentation is absent in other material. None of the paratype material was gravid i.e. contained coelomic gametes. The additional material examined exhibited some variation in the development of the lateral lobes on segment 3. The material from Western Australia has a larger dorsal extension of the lobe on segment 3 than other material examined. However in all other respects the Western Australian material resembles the type material. The material collected from Ship Rock, Port Hacking has only 16 notopodia on one side, and 17 on the other side. All the other material examined has 17 pairs of notopodia.

Comments. *Lanicides tribranchiata* n. sp. appears to have a fairly wide subtidal distribution in Western Australia, Victoria and New South Wales. It has not been collected from South Australia where almost no offshore collecting has been done. *Lanicides tribranchiata* has three pairs of branchiae whereas all other described species have only two pairs of branchiae.

Lanicides tribranchiata has very heavily chitinised anterior uncini in contrast to the other two Australian species of *Lanicides* and may belong to a group of species currently within the genus *Pista* (Hutchings, in prep). The structure of the notosetae of *L. tribranchiata* (Fig. 9d,e), is slightly different to *L. lacuna* (Fig. 9a-c) a more typical species of *Lanicides*.

Etymology. The specific name *tribranchiata* refers to the three pairs of branchiae present.

Habitat. Found subtidally in depths of 3–40 m, with a firm sandy tube attached to solid substrates.

Distribution. Western Australia, Bass Strait, Victoria, New South Wales.

Lanicola Hartmann-Schröder

Lanicola Hartmann-Schröder, 1986: 58; 1987: 58.

Eye spots absent. Branchiae, 2 pairs on segments 2 and 3, branched. Thorax with 17 pairs of notopodia from segment 4; notosetae smooth-tipped capillaries. Abdomen long with numerous segments. Neuropodia from segment 5 (setiger 2), uncini arranged in double rows face to face in posterior thorax. Lateral lobe present on segment 3.

Type species. *Lanicola lobata* Hartmann-Schröder, 1986, by original designation.

Lanicola lobata Hartmann-Schröder

Lanicola lobata Hartmann-Schröder, 1986: 56; 1987: 58.

Material examined. South Australia, Wallaroo, 3(HZM P18631).

Description. Prostomium compact, with eye spots. Branchiae, 2 pairs on segments 2 and 3, each

branchiae with few dichotomous branches. Notopodia from segment 4, 17 pairs, notosetae smooth-tipped capillaries. Neuropodia from segment 5 (setiger 2), uncini initially arranged in single rows, in posterior thorax uncini arranged in double rows, face to face. Uncini avicular with dental formula MF:4-5:7:~10 on first uncinigerous segment to MF:3:6:8:α on middle thoracic segments. Peristomium expanded to form small laterally positioned lobe. Lateral lobe present on segment 3,

lobe elongate rectangular in shape, connected midventrally. Nephridial papillae present on segments 3, 4, 6 and 7.

Comments. This species closely resembles *Lanicides fascia*, in the development of a lateral lobe on segment 3 but differs in the development of the uncini of the first uncinigerous segment. At this stage the genus is known only from south-western Australia and Victoria.

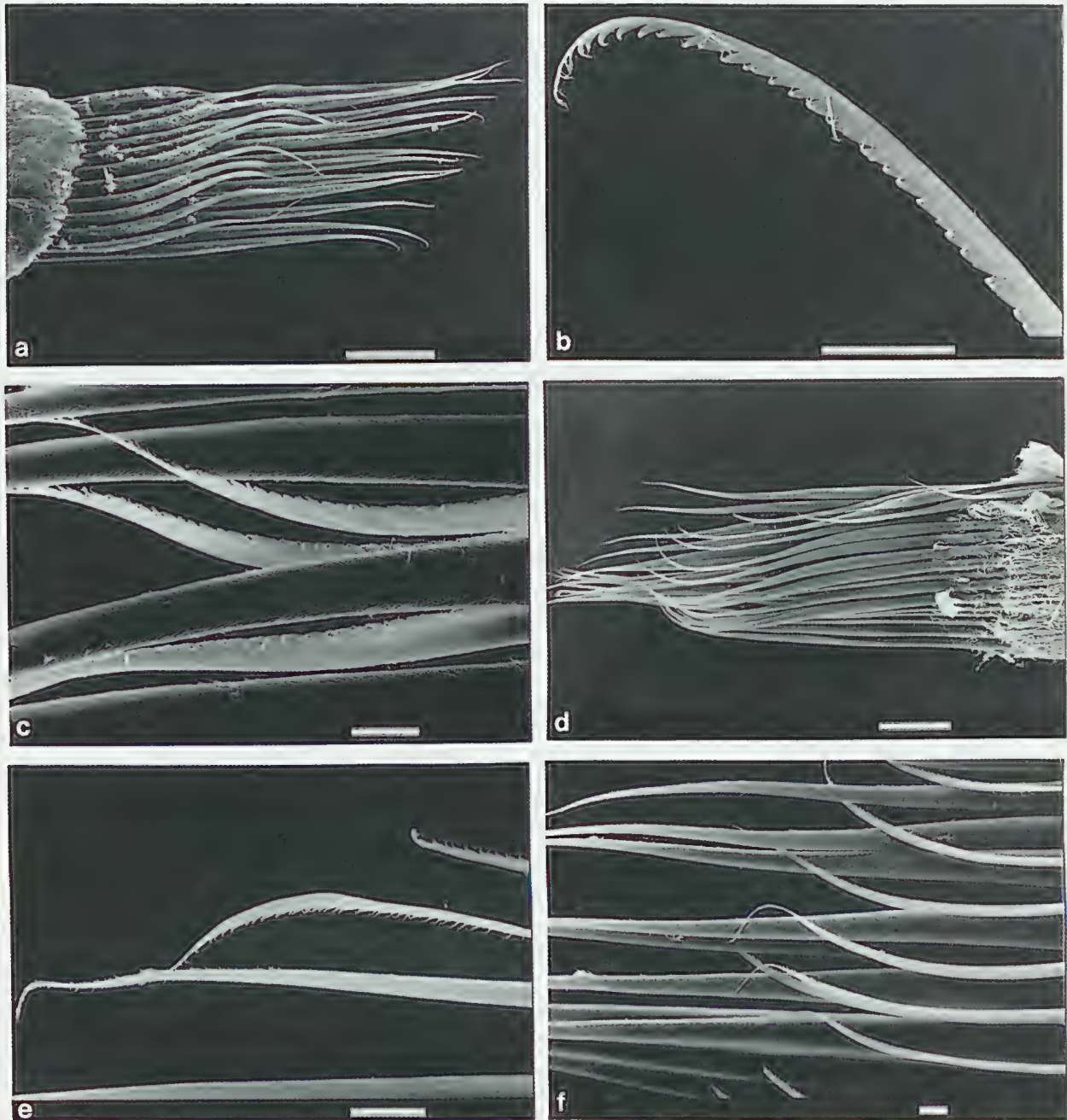


Fig.9. *Lanicides lacuna* n. sp. a. SEM x190 showing 2 kinds of notosetae; scale is 100 μm. b. SEM x3000 showing serrations on notoseta; scale is 10 μm. c. SEM x1500 showing smooth and serrated notosetae; scale is 10 μm. *Lanicides tribranchiata* n. sp. d. SEM x160 showing 2 kinds of notosetae; scale is 100 μm. e. SEM x1600 showing 2 kinds of setae; scale is 10 μm. f. SEM x650, scale is 10 μm.

Habitat. Found among algae on boulders, intertidally.

Distribution. South Australia (Wallaroo), Victoria.

Loimia Malmgren

Loimia Malmgren, 1866: 380.—Hessle, 1917: 170.—Fauchald, 1977: 131.

Branchiae, 3 pairs, dichotomously branched on segments 2, 3 and 4. Lateral lobes present anteriorly from peristomium. Notopodia from segment 4, 17 pairs; notosetae smooth tipped. Neuropodia from segment 5 (setiger 2); uncini with teeth arranged in a vertical series in adults. Uncini arranged in double rows, back to back, on midposterior thorax.

Type species. *Terebella medusa* Savigny, 1818, by monotypy.

Comments. We have modified the generic description of *Loimia*, stating that uncini with teeth arranged in a vertical series are present only in adults. The thoracic uncini of young animals of some species have more than one row of teeth near the apex (Gravier, 1906; Fauvel, 1907; this paper) while abdominal uncini in young *L. ingens* have a considerable number of teeth arranged in a transverse series (this paper). Wilson (1928) also found that some abdominal uncini of *L. medusa* around 1.0–1.5 cm long have more than one row of teeth near the apex, however thoracic uncini were of the adult type.

In addition to the intraspecific dental variation present in *Loimia*, the form of the upper base of the uncini also varies with age. The uncini of young individuals of both *L. medusa* and *L. ingens* have a prominent, anteriorly directed ligament on the upper base of the uncini which is subsequently lost as the individual ages. In very large specimens of *L. ingens* a similar ligament is also present on the uncini. It would appear therefore that until the ontogeny of *Loimia* species is known, the form of the uncini is of

limited value as a specific character. This factor, together with the rather constant form of the notosetae found in all species of *Loimia* makes the taxonomy of this group difficult.

The genus *Loimia* contains *L. medusa* (Savigny, 1818), which is recorded as a cosmopolitan species, and several species with very restricted distributions. As no adequate description of *L. medusa* exists, a full description of this species based on material from the type locality is being prepared for publication (Hutchings & Glasby, in prep). We suspect that *L. medusa* is not a cosmopolitan species and all records of *L. medusa* from Australia have been referred to *L. batilla* n. sp. Grube (1878) described five species from the Philippines which represents nearly one third of the known species of *Loimia*. Material of four of these species [*L. annulifilis* (MPW – type and non type material ZMB 920); *L. crassifilis* (MPW 309 – type and probably non type material ZMB Q5635); *L. montagui* (MPW 404); *L. variegata* (MPW – type and non type material ZMB Q4968, ZMB 522, ZMB 519)] has been examined and all is in poor condition. The type of *L. variegata* (ZMB 519) has a locality given as the Red Sea in the vial, whereas Grube (1878) gives the type locality as the Philippines. This material is not a species of *Loimia*, however the rest of the material examined of *L. variegata* does belong to the genus. So at this stage most of the species of *Loimia* described from the Philippines pose problems, especially in identifying species of *Loimia* from the Indo-Pacific.

Presently, there are four species of *Loimia* found in Australian waters – *L. batilla* n. sp. and *L. triloba* n. sp. which each have a fairly restricted geographical distribution, and *L. ingens* which is recorded throughout much of Australia. *Loimia ochracea* Grube, 1877 described from north-west Australia has not been recorded since its original description. We have split the *Loimia* species present in Australian waters, primarily on the development and structure of the lateral lobes which we believe are very important characters in the genus *Loimia*.

Key to the Australian species of *Loimia*

1. A pair of small lateral lobes on segment 4. *L. triloba*
 — Lateral lobes on segment 4 absent. 2
2. Lateral lobes, 2 pairs, on segments 2 and 3 *L. ochracea*
 — Lateral lobes, 1 pair, arise from junction of segments 2 and 3 3
3. Lateral lobes on segments 2/3 extending ventrally to form an anteriorly projecting scoop. *L. batilla*
 — Lateral lobes on segments 2/3 discrete, not continuous with ventral lobe *L. ingens*

Loimia batilla n. sp.

Fig. 10a–f

Loimia medusa.—Stephenson et al., 1974: 113.—
Hutchings, 1977: 19. *Non Savigny*, 1818.

Material examined. HOLOTYPE: Queensland: Moreton Bay, south of Peel Island, Stn III B3 20°26'S, 147°05'E (AM W5162), specimen complete consisting of 2 fragments, made up of 68 segments, about 47 mm long, 6.0 mm wide, mature. PARATYPES: Moreton Bay, south of Peel Island 1(AM W5094), 1(AM W5088), 1(AM W7107); Middle Banks off Tangalooma 1(AM W7097), 1(AM W7098), 3(AM W7099), 6(AM W7100), 1(AM W7101), 1(AM W7102), 2(AM W7103), 1(AM W7104), 3(AM W7105), 3(AM W7106), 1(AHF Poly 1470), 1(BMNH ZB 1986.71), 1(USNM 99973). Paratypes mostly incomplete, range in width from 2.1–6.6 mm wide.

Additional material examined. Queensland, mouth of Brisbane River 1(QM GH3434).

Description. Tentacles with thin black bands, otherwise preserved body unpigmented. Anterior body highly muscular, slightly dorsoventrally compressed, first 11 segments very short with each parapodium in this region touching adjacent ones. Dorsally, pair of white, glandular ridges extends over first 10 segments, just above notopodia. Posterior thoracic segments longer than anterior thoracic segments, body widest over midposterior thorax, tapering gradually over abdominal segments. Last few segments highly tapering in width, presumably representing regenerating posterior end.

Prostomium very short, collar-like, eyespots absent. Peristomium very short dorsally, about half

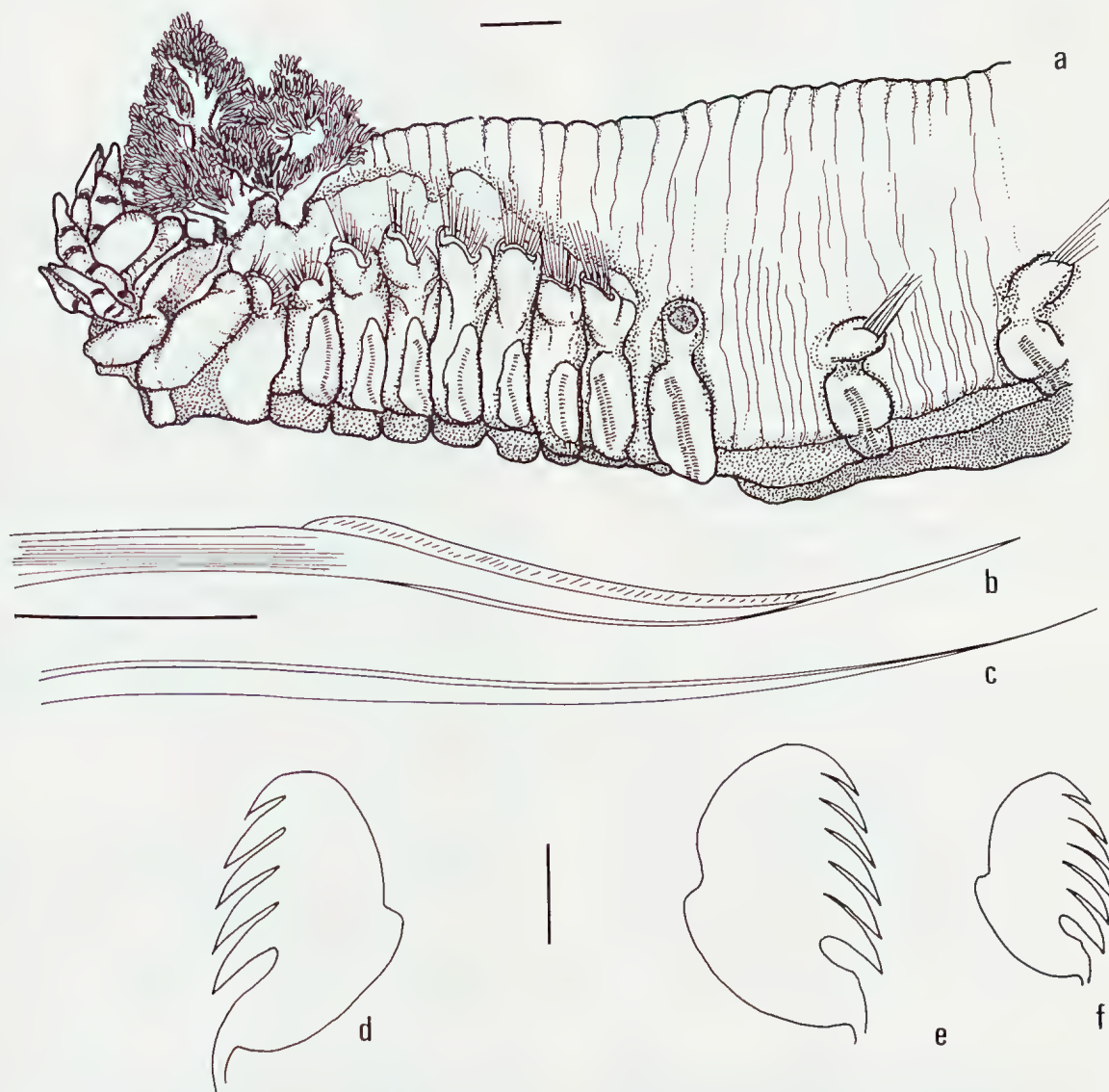


Fig. 10. *Loimia batilla* n.sp., holotype. a. lateral view, anterior body scale is 1 mm. b. notoseta from setiger 5, scale is 0.1 mm. c. notoseta from setiger 5, scale is 0.1 mm. d. thoracic uncinus, scale is 0.01 mm. e. uncinus from anterior abdominal setiger, scale is 0.01 mm. f. uncinus from midabdominal setiger, scale is 0.01 mm.

length of segment 2; laterally expanded as pair of prominent lobes which unite ventrally forming anteriorly directed scoop which partially covers oral cavity. Segments 2 and 3 fused laterally forming pair of lateral lobes which extend ventrally to form glandular scoop. Branchiae 3 pairs on segments 2–4, third pair arise dorsally to notopodia on segment 4. First pair of branchiae about twice size of second and third pair of branchiae; each with thick main stem, branches with spirally whorled filaments distally (Fig. 10a).

Notopodia from segment 4, 17 pairs; first 8 pairs of podia thick, cylindrical, following ones slender, slightly longer than anterior ones. Notosetae consist of 2 types; thick, broad-winged capillaries, slender, narrow-winged capillaries; anterior notosetae shorter, more robust than posterior ones (Fig. 10b,c). Neuropodia from segment 5 (setiger 2), continuing to near pygidium; podia sessile glandular ridges on thorax, abdominal neuropodia elongate pinnules, similar in length to thoracic neuropodia. Thoracic uncini with 5–6 teeth arranged in vertical series, slight protruberance sometimes present on base below teeth (Fig. 10d); abdominal uncini similar in shape, dentition but smaller in size than thoracic ones (Fig. 10e,f). Uncini arranged in single row to segment 10 (6th uncinigerous segment), from segment 11–20, uncini in double rows arranged back to back, thereafter uncini arranged in single row to pygidium.

Ventral glandular pads to segment 12, thereafter shallow glandular streak; pads on segments 2–4 fused, with anterior edge of segment 2 forming anteriorly directed scoop. Nephridial papillae minute conical processes on segment 3, segments 6–8; anterior pair located on posterior edge of segment, lateral to base of branchiae, posterior pairs present at posterodorsal base of notopodia.

Pygidium with 7 large papillae encircling terminal anus.

Variation. The paratypes vary from the holotype as follows: – tentacular pigmentation may be absent; anterior segments sometimes not dorsoventrally compressed and without excessively shortened segments, dorsal glandular ridges extend to segments 8 to 10; branchiae with first pair one to two times larger than subsequent pairs; uncini with 5 to 7 teeth in a vertical series, the number appearing to be independent of the size of the animal; nephridial papillae absent in smaller specimens; pygidium with 6 anal papillae in one specimen.

Tube consists of fine, flocculent material covering an inner lining of mucus.

Comments. Material identified by Hutchings (1977) as *L. medusa* is synonymous with *L. batilla* n. sp. This species may be distinguished from other species of *Loimia* in having the fused lateral lobes on segments 2 and 3 extending ventrally as a distinct scoop.

Etymology. The specific name is derived from the latin *batillum*, a shovel, referring to the scoop-shaped anterior ventrum.

Habitat. The species is widespread in Moreton Bay, occurring in fine sand-mud, at depths of 4–12 m.

Distribution. Queensland (Moreton Bay). Williams (pers. comm.), who reviewed an early draft of this paper has apparently found this species in Borneo using the above description.

Loimia ingens (Grube)

Fig. 11a–l

Terebella ingens Grube, 1878: 228–230, pl. 13, fig. 1.

Loimia ingens.—Hessle, 1917: 170.—Hutchings, 1977: 18.

Loimia nr. *ingens*.—Hartman, 1966a: 364, pl. 38a,b.

Loimia medusa.—Augener, 1922: 46–48; 1927: 253–254.—Hartmann-Schröder, 1979: 147–148. *Non* Savigny, 1818.

Loimia montagui.—Monro, 1931: 29. *Non* Grube, 1878.

Material examined. Western Australia: Admiralty Gulf 1(AM W200467); Rowley Shoals, east side of Clerke Reef 1(WAM 56-84); North West Shelf, off Port Hedland 1(AM W200469), 1(AM W200470); Warroora 2(AM W5446); Rottneest Island 1(WAM 26-73). South Australia: Kangaroo Island, Penneshaw Jetty 1(AM W200466); Upper Spencer Gulf 1(AM W5976). New South Wales: Botany Bay, Quibray Bay 2(AM W196825); Port Jackson (ZMC); Pittwater, Careel Bay 5(AM W194081); Port Stephens 1(AM G11200), 1(AM W5163); South West Solitary Island 1(AM W200554). Queensland: Moreton Bay, south of Peel Island, Stn II B3 1(AM W7990), (AM W5090); Hervey Bay 5(AM W5387); Gladstone, Auckland Creek 1(AM W198248); Great Barrier Reef, North West Pine Island 1(AM W200528), Magnetic Island 3(AM W200545), Great Palm Island 1(AM W200531), Lizard Island 1(AM W200525), 1(AM W200526), 1(AM W200520), 1(AM W200524), 1(AM W200532), Thursday Island 2(AM G11195); Gulf of Carpentaria, West of Burrowes Point 4(AM W200535). Northern Territory: Gove 1(NTM W1323); Port Essington, Table Head 1(NTM W139), Coral Bay 1(NTM W129); Darwin, Fannie Bay 1(AM W200555). A selection of material examined, ranged in width from 0.5–17 mm.

Comments. Examination of a large amount of *Loimia* material of different sizes throughout Australian waters revealed considerable variation. Currently we cannot determine if this variation is due to the presence of subspecies or if characters just vary with size. We therefore regard *Loimia ingens* as a species complex. The species complex is characterised by: the absence of prostomial eyespots; two pairs of well-developed lateral lobes on the peristomium, and a pair arising from the junction of segments 2 and 3; three pairs of branchiae in which terminal filaments are arranged spirally; 17 pairs of notopodia and adult uncini with three to seven teeth arranged in a vertical series, and uncini which are arranged in double rows from segments 11 to 20. The

material examined varies in the degree of pigmentation present. This ranges from pigmentation being totally absent or restricted to banded tentacles, to heavy body pigmentation of mottled brown on thorax, dorsum and abdomen and solid brown on ventral pads. The size and shape of lateral lobes also varies, and this appears to be affected by the state of contraction of the head end.

Other characters which vary are the size and degree of branching of the branchiae and the dental formula and shape of the base of the uncini.

The lateral lobes on the peristomium (segment 1) extend ventrally to form one continuous lobe. The degree of development and anterior extension of this lobe varies in the material examined from the lobe completely covering the oral cavity and base of the



Fig. 11. *Loimia ingens*. Specimen from Lizard Island, 2.1 mm width (AM W200525). a-d. uncini from one row, early precursor, late precursor, first fully formed, and mid row fully formed uncini, respectively, scale is 0.1 mm. Specimen from Moreton Bay (AM W5090), 3.6 mm width. e-h. early precursor, late precursor, first fully formed and mid row fully formed uncini. i-l. North West Shelf specimen, 0.5 mm (AM W200469), uncini from midthoracic segment, (i) and frontal views (j), uncini from midabdominal segment, side (k) and frontal (l) views, scale is 0.01 mm. m-o. Specimen from Rottnest Island (WAM 26-73), 15 mm width, mid late precursor (m), side view, first fully formed uncus, side view (n), mid row fully formed uncus, side view (o), scale is 0.1 mm.

buccal tentacles to being in a retracted state, recurved backward and exposing the oral cavity. Variation in this latter character appears to be size related. It appears that the lateral lobes of segments 2 and 3 have become fused to form a single lobe, and arise from the junction of segments 2 and 3. This will need to be confirmed by sectioning some material or following the development of lateral lobes from metamorphosis onwards.

The number of teeth in the vertical series of the thoracic uncini is fewest in small specimens of less than 1.0 mm in width (average numbers of teeth per uncini is 4.7) (Fig. 11i-l). The largest number are found in small to medium sized specimens of 2-10 mm in width (av. 5.35) (Fig. 11e-h). The number of teeth is less in specimens of 11 mm in width or larger (av. 4.40) (Fig. 11m-o). In one very small specimen, 2.5 mm long and 0.5 mm in width (AM W200469) (Fig. 11i-l) thoracic uncini have teeth arranged in more or less a vertical series with dental formula of MF:1:1-2:1:1-2:0-1, whereas abdominal uncini have teeth arranged in a transverse series above a MF with dental formula MF:1:2-6:3-7:α. Such a difference in the dental formula and arrangement of teeth within a specimen was not observed in larger animals. In addition to the variation in the dental formula, the smallest and the largest specimens often have a well-developed subrostral ligament below the teeth (Fig. 11i) which is often absent or extremely reduced in the small to medium sized specimens (Fig. 11f). Both these types of uncinal variations were present in the Lizard Island specimens which ranged from 0.8-6.2 mm in width (Fig. 11a-d) and in the North West Shelf specimens which varied from 0.5-2.2 mm in width (Fig. 11i-l).

Earlier authors have remarked on the great variability of the shape and dentition of the uncini of *Loimia medusa* Savigny, both within and between individuals (Gravier, 1906; Fauvel, 1914; Wilson, 1928). Adult and juvenile uncini described by Gravier (p. 224, figs 396-399) are similar in shape and dentition to the thoracic uncini from juvenile and small to medium sized specimens in the material of *L. ingens* examined. Fauvel (1914) suggested that the subrostral ligament in the uncini of juvenile *L. medusa* disappears with wear. In *L. ingens* however we feel that the presence or absence of the subrostral ligament is predetermined in the development of the animal, just as is the number of teeth in the uncini.

To test this hypothesis we examined the shape of the uncini in neuropodia from several different sized animals of Thelepodinae, paying particular attention to the shape of newly formed uncini in the precursor region of each row (Hutchings & Glasby, 1987). We found no evidence of any significant difference in the shape of the basal portion of the uncini. Most uncini are either formed with or without a subrostral ligament, but some uncini are characterised by an intermediate condition which does change noticeably with growth. Hence the importance of

wear in determining the shape of the uncini, and specifically the size of the subrostral ligament, is considered less important than genetic factors.

We examined a specimen identified by Hartman (1966a) as *L. nr. ingens* (AM W3803) and have referred it to *L. ingens*. Similarly we examined material identified by Monro (1931) from the Great Barrier Reef Expedition as *L. montagui* (BMNH 1931.7.1.63) and have also referred this to *L. ingens*.

Habitat. Found in marine-sheltered estuarine embayments, from intertidal to 100 m; in mud-sand, associated with *Posidonia* in Botany Bay, Careel Bay and Port Stephens, on rocks embedded in mud and from coral reef flats under dead coral.

Distribution. Australia (widespread, north of 36°S lat.)

Loimia ochracea (Grube)

Terebella (Loimia) ochracea Grube, 1878a: 547-548.

Material examined. Western Australia: Mermaid Cove. HOLOTYPE (ZMB 906); (MPW 583).

Two lots of material labelled as *L. ochracea* by Grube have been found. One vial from the Muzeum Przyrodnicze in Wroclaw consists of odd fragments and could not be positively identified as belonging to a terebellid. The other material also labelled as type in the Zoologisches Museum, Berlin is incomplete posteriorly, but is certainly a species of *Loimia*, and is described below.

Description. Type incomplete posteriorly with maximum width of 6.7 mm. Large parts of thoracic epidermis have been removed. No branchiae or buccal tentacles remain. Three pairs of branchial scars on segments 2, 3 and 4, with first pair of scars inserted most dorsally.

Peristomium with no lateral expansion to form lobes. Segment 2 with small rounded ventrolateral lobe connected midventrally by U-shaped connecting ridge. Segment 3 with small semi-spherical lobe directed at angle dorsolaterally.

Notopodia begin on segment 4, as all setae have been shaved off, it is not possible to count total number of pairs of notopodia. Uncini begin on segment 5 (setiger 2), uncini have 5 teeth above main fang in single row. Abdominal neuropodia rectangular erect podia.

Thoracic ventral glandular pads discrete and rectangular. No pigmentation present.

Comments. No additional records of this species have been reported and it appears to differ from all of the other described species of *Loimia* from Australia.

Habitat. Unknown.

Distribution. Western Australia (Mermaid Cove).

Loimia triloba n. sp.

Fig. 12a-d

Material examined. HOLOTYPE: Queensland: Great Barrier Reef, Three Isles, 15°07'S, 145°26'E, (BMNH ZB

1986.97), Stn 3.2, coll. no. 268, complete, 158 segments, 107 mm long, 3.8 mm wide. PARATYPES: Great Barrier Reef, Three Isles, Stn 3.1, coll. no. 261, 1(USNM 99974); Low Isles, 16°23'S, 145°34'E, Stn L5, coll. no. 181, 1(AHF Poly 1471), Stn L6, coll. no. 196, 1(AM W200558), Stn L6, coll. no. 199, 3(BMNH ZB 1986.100-102), Stn L3, coll. no. 155, 2(BMNH ZB 1986.98-99), Stn K7, 11°40'S, 144°00'E 5(BMNH ZB 1986.103-107). Paratypes range in width from 0.9–4.0 mm.

Additional material examined. Queensland: One Tree Island, lagoon (AM W200555).

Description. Body with short, robust thorax, long, wide abdomen, mainly unpigmented except for some bluish pigment on lateral borders of midventral glandular pads. Segments 2–12 glandular where branchiae, and notopodia arise. Prostomium short, compact with inflated upper lip extending anteriorly. Buccal tentacles largely missing. Eyespots dark, arranged in 2 very short rows on either side of posterior prostomium, partially obscured by posterior deflection of collar. Peristomium about half the length of segment 2 dorsally, anterior edge

thickened, elevated slightly; laterally, anterior edge expanded forming pair of well-developed lateral lobes which extend ventrally. Lateral lobes on segment 2 or 3 smaller, angular, not extending ventrally, the exact segmental origin of this lobe cannot be determined, it appears to arise from junction of these 2 segments. Segment 4 with very small, elongate lobe, located just below first pair of notopodia. Branchiae 3 pairs, on segments 2–4, arise dorsally to line of insertion of notopodia, first pair of branchiae about twice as large as subsequent ones; each with thick main stalk, dendritic branching subdistally, distally loosely spiralled filaments (Fig. 12a).

Notopodia from segment 4, 17 pairs; podia short, rectangular, similar-sized throughout. Noto setae consist of winged capillaries of 2 lengths, shorter ones with transparent wing (Fig. 12b,c). Neuropodia from segment 5 (setiger 2), extend to pygidium; podia sessile, glandular ridges on thorax, elevated pinnules on abdomen, similar sized throughout, except on last few segments which are regenerating, podia are

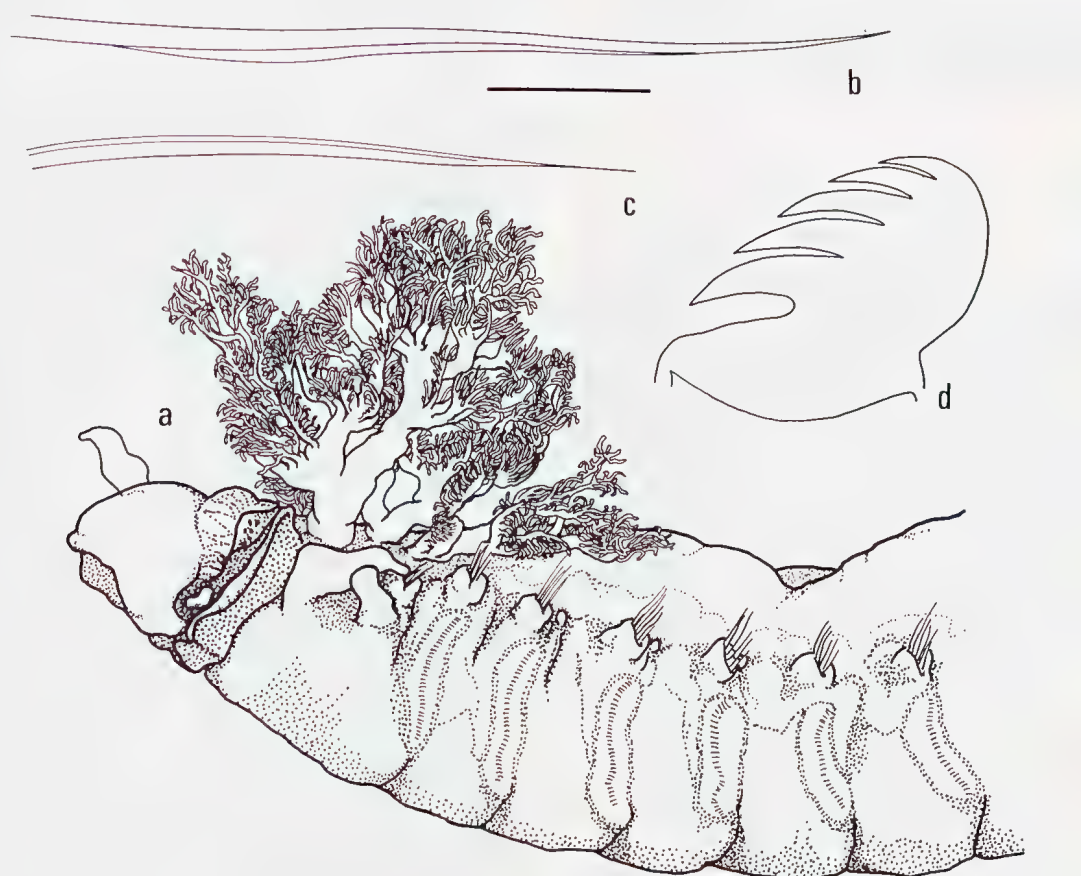


Fig. 12. *Loimia triloba* n. sp., holotype (BMNH ZB 1986.97). a. lateral view, anterior body, scale is 1 mm. b. long notoseta from setiger 5, scale is 0.1 mm. c. short notoseta from setiger 5, scale is 0.1 mm. d. uncinus from midthoracic segment, scale is 0.01 mm.

minute. Uncini with 5 teeth in vertical series, smooth upper base, similar shape throughout (Fig. 12d). Uncini arranged in single rows to segment 10, on segments 11–20 arranged in double rows, back to back, thereafter in single rows to pygidium.

Midventral glandular pads present to segment 14, last few heavily dissected, pads on segments 2–4 fused. Nephridial papillae minute, on segments 3, and 6–8, first pair just ventrolateral to branchiae, remainder posterodorsal to notopodia.

Pygidium with about 15 elongate papillae encircling terminal anus.

Variation. Paratypes generally unpigmented, except for 1 complete specimen with a brown pygidium, and some with bluish pigment on the midventral pads to segment 11. Lateral lobes on peristomium well developed ventrally in smaller specimens extending anteriorly to cover base of buccal tentacles, in larger specimens lateral lobe poorly developed ventrally like holotype. Lateral lobes on segment 4 absent in smallest specimens. Branchiae with first pair 1–2 times larger than subsequent ones, smaller specimens with fewer branchial filaments than larger specimens. Uncini with 5 or 6 teeth in a vertical series, smooth slightly humped upper base, without well-developed ligament. Midventral glandular pads to segment 12–15. Nephridial papillae absent in smallest specimens. Pygidium with 3 very long anal cirri in 1 complete specimen.

Comments. *Loimia triloba* n. sp. may be distinguished from *L. batilla* n. sp. and *L. ingens* by the presence of eyespots and a pair of small lateral lobes on segment 4. These lobes appear to be present on all but the very smallest specimens (width of body < 1.0 mm), and increasing in size in relation to the other lobes as the worm grows. This situation appears opposite to that recorded by Gravier (1906) for *L. medusa* in which a lobe on the third segment (presumably segment 4 in our scheme) is present in the young but not in the adults.

Etymology. The specific name *triloba* refers to the three pairs of lateral lobes on the anterior segments, and is made of *tri* meaning three and *lobus* meaning lobe, which was changed to *loba* as the gender of genus *Loimia* is feminine.

Habitat. Found intertidally to depths of 22 m in sediment ranging from muddy sand to medium coarse sand.

Distribution. Queensland (Great Barrier Reef).

Longicarpus Hutchings & Murray

Longicarpus Hutchings & Murray, 1984: 97.

Branchiae, 3 pairs on segments 2, 3 and 4, dichotomously branched. Lateral lobes poorly developed. Notopodia from segment 4, about 23 pairs; notosetae distally serrated. Neuropodia with uncini from segment 5 (setiger 2), arranged in double

or alternate rows from segment 10 or 11; anterior thoracic uncini with well-chitinised shafts. Nephridial papillae from segment 3.

Type species. *Longicarpus glandulus* Hutchings & Murray, 1984 (= *L. modestus*) by original designation.

Comments. *Longicarpus* is similar to the genera *Amphitrite* and *Terebella*, in having lateral lobes intermediate between the two. It differs in having long-handled uncini present on anterior segments. It also superficially resembles the genus *Pista* as discussed by Hutchings & Murray (1984). A recent study by Hutchings (in press) of the terebellids of Hong Kong has recorded another species of *Longicarpus* in the harbour of Hong Kong.

Longicarpus modestus (Quatrefages)

Terebella modesta Quatrefages, 1865: 365.

Amphitrite rubra.—Fauvel, 1917: 265–267, fig. 27a–f.—

Knox & Cameron, 1971: 36 (in part). *Non* Risso, 1826.

Longicarpus glandulus Hutchings & Murray, 1984: 97, fig. 28.1–5.

Material examined. Western Australia: Houtman Abrolhos, Long Island 1(WAM 50-84); Cockburn Sound 1(WAM 32-84), Rottnest Island (AM W201039); Bunbury 1(NTM W2423). South Australia: West Lakes 4(AM W200177); Coffin Bay 1(AM W200174); Upper Spencer Gulf 1(AM W5978); Kangaroo Island, Penneshaw Jetty 2(AM W200172); Sellicks Beach 1(AM W200173). Tasmania: Norfolk Bay, near Eaglehawk 1(AM W200171), Grassy Harbour, King Island 1(NMV unreg), St Helen's, north-east Tasmania (NMV unreg); south-east Tasmania, Midway Point (TASM K1022). Bass Strait: Stn 212 1(NMV unreg), 1(NMV unreg). Victoria: Portland Pier, several(NMV unreg); Mallacoota Inlet 1(AM W200175); Gabo Island 1(AM W200169), 1(AM W200170). New South Wales: Green Cape 1(AM W200164); Jervis Bay, Darling Down 3(AM W200159); Port Hacking, Ship Rock 4(AM W200155); Long Reef 2(AM W200154). Queensland: One Tree Island, lagoon 1(AM W200430). A selection of material examined, size ranged from an incomplete specimen 1.0 mm wide to a complete specimen, 72 mm long, 8.0 mm wide, and about 100 segments.

Variation. We have examined a large number of specimens and found additional variations to those described by Hutchings & Murray (1984). This included the colour in alcohol, from pale cream to brown, sometimes with additional rust-red pigment on thorax; 21–24 pairs of notopodia; uncini with a subrostral guard, arranged in a single row from segments 5–10, then in an alternate row to segments 50–58, then in a single row once more to the pygidium; dental formula of uncini MF:3-5:3-9:10-20:α. Nephridial papillae on segments 3–8 at ventral base of notopodia, decrease in size posteriorly, smaller specimens with fewer pairs.

Comments. The type specimen of *Terebella modesta* Quatrefages examined by us, was one of a number of specimens described by Quatrefages

(probably syntype 1 [MNHN No. 276a]) from Jervis Bay, albeit in a very incomplete way. The specimen agrees well with the present material. We also examined the holotype of *Longicarpus glandulus* Hutchings & Murray (AM W19532) and found it to be synonymous with Quatrefages' species. Hutchings & Murray (1984) give a detailed description of the species which is characterised by having diffuse glandular areas on anterior segments, rather than discrete lateral lobes and long handled anterior thoracic uncini. We have therefore synonymised *L. glandulus* with *Terebella modesta*.

The previously known distribution of *Longicarpus modestus* has been considerably expanded.

Habitat. Occurs from lower intertidal zone to 28 m on exposed rocky coasts under stones, attached to boulders, associated with sponge beds, macroalgae holdfasts and dead coral on reef crests. Also occurs in sheltered bays in sandy sediment, sometimes associated with scallop and mussel clumps, to 30 m. In life, the animal is bright red with orange tentacles and bright red branchiae.

Distribution. Western Australia, South Australia (widespread), Tasmania, Victoria, New South Wales (widespread), Queensland.

Neoleprea Hessle

Neoleprea Hessle, 1917: 191–192, fig. 47.

Branchiae, 2 pairs on segments 2 and 3, dichotomously branched. Lateral lobes absent. Notopodia from segment 3, continue for a variable number of segments; notosetae distally serrated. Neuropodia with uncini from segment 5 (setiger 2), arranged in double rows face to face from midthorax. Nephridial papillae numerous, from segment 3 or segment 6.

Type species. *Leprea streptochoeta* Ehlers, 1897 designated by Hessle, 1917.

Comments. There has been some confusion over the numbering of the branchiferous segments in *Neoleprea* and this has led to confusion as to the segment on which the notopodia first occur. The type species, *Neoleprea streptochoeta* (Ehlers) (Port Stanley, Falkland Islands, SYNTYPES 8(HZM V4931); coll. 17.VII.1893), has 2 pairs of branchiae on segments 2 and 3, notopodia from segment 3 and neuropodia from segment 5. All other existing species of *Neoleprea* (*N. californica* (Moore, 1904) San Diego County, California, HOLOTYPE (CAS 019704), *N. amoyensis* Monro, 1934, Amoy, China, HOLOTYPE (BMNH 1933 3.2.41); coll. T.Y. Chen; *N. clavata* Mohammed, 1973, Mena Abdullah, Kuwait, 29°01'N, 48°10'E, HOLOTYPE (BMNH ZB 1971.57); coll. 10 October, 1969 from intertidal zone under rock), with the exception of *N. japonica* Hessle, 1917, and perhaps *N. spiralis* Johnson, 1901, have the same arrangement of branchiae and podia as the type species and constitute a monophyletic group. The

holotype of *N. spiralis* (HOLOTYPE [MCZ 1874] Puget Sound, Washington, coll. A. Robertson, 1898), is in poor condition and it is not possible to ascertain for certain which segments are branchiferous, however some later descriptions of the species (Berkeley & Berkeley, 1952) give the branchiferous segments as 2 and 3 rather than 3 and 4 as stated by Johnson, 1901. The syntypes of *N. japonica* were re-examined (SYNTYPES 1[SSM unreg] Sagami Yokuskastrasse, [this name not found in Atlas, may refer to Sagami Bay south of Tokyo near Yokusuka] 135 m, 19/6; 1[SSM unreg] Sagami Misaki, 150 m, 11/6; 1[SSM unreg], Sagami Okinose, 500 m, 30/6; coll. S. Bock, 1914), and found to have branchiae on segments 3 and 4, i.e. two pairs of branchiae, notopodia from segment 4 and neuropodia from segment 6. Similarly, specimens of *N. streptochoeta* non Ehlers identified by Hessle (1917) (Falkland Islands SYNTYPES 1(SSM 2169) 51°33'S, 58°10'W, 7 m; 1(SSM 2171), 58°42'S, 57°50'W, 10 m; coll. Svenska Syd-polar Expedition 1901–1903), have the same arrangement. It would appear that these specimens have been wrongly labelled as syntypes of *N. streptochoeta*.

Neoleprea japonica and Hessle's material of *N. streptochoeta* cannot be assigned to any described genus of terebellid. We are reluctant, however, to describe this material as a new genus, as it is not in good condition.

Neoleprea macrocercus n. sp.

Fig. 13a–g

Material examined. HOLOTYPE: New South Wales, Diggers Camp, between Minnie Water and Woolli, 153°17'E, 29°19'S, (AM W200340); posteriorly incomplete, 111 segments, 43 mm long, 2.1 mm wide. PARATYPES: 2(AM W200342), 1(AM W200341), 1(AHF Poly 1472), 1(BMNH ZB 1986.72), 1(USNM 99975), collection details as for holotype; range in size from 2.0 mm wide to a complete specimen of 102 segments, 36 mm long, 2.4 mm wide.

Additional material examined. Victoria, west of Eagles Nest, 1(NMV unreg). New South Wales: west side of South West Solitary Island 1(AM W200343).

Description. Body inflated anteriorly, widest over first few segments tapering gradually to long uniformly wide abdominal region. Tentacular lobe collar like, produced anteriorly as short, smooth, sloping upper lip, deeply cleft medially as result of damage. Buccal tentacles filiform, grooved. Eyespots faint, arranged in 1 irregular row across posterior tentacular lobe. Peristomium about length of segment 2 dorsally, ventrally forming broad lower lip with deep transverse groove separating inner, outer parts. Branchiae, 2 pairs on segments 2 and 3, equal in size, arise laterally just above line of notopodia (Fig. 13a). Branchiae dendritically branched with short stalk, branches decreasing in thickness gradually outward.

Notopodia from segment 3 extend for 28 or 29 segments; podia short, tapered, becoming more pointed posteriorly (Fig. 13b,c). Notoetae arranged in 2 tiers of 2 types of setae, long, narrow-winged, distally hispid capillaries, shorter, hispid, slightly flagged types (Fig. 13d,e). Neuropodia from segment 5 (setiger 3) present on all following segments; podia low, elongate ridges throughout, length of ridges

decreasing posteriorly. Uncini with small, anteriorly projecting subrostral ligament (Fig. 13f), dental formula MF:4-6: 5-7:10-17; arranged in single rows to segment 8, thereafter uncini arranged in double rows to end of body, face to face (Fig. 13g).

Midventral glandular pads on segments 2-15, first few pads yellowish, then becoming white. Midventral glandular groove extends from segment



Fig. 13. *Neoleprea macrocercus* n. sp., holotype. a. lateral view, anterior body, scale is 1 mm. b. notopodia from segment 4 (left side) anterior view, scale is 0.1 mm. c. notopodia from segment 24 (left side) anterior view, scale is 0.1 mm. d. long notoseta from setiger 4, scale is 0.1 mm. e. shorter notoseta from setiger 4, scale is 0.1 mm. f. uncinus from segment 11, scale is 0.01 mm. g. uncinus from midposterior body segment, scale is 0.01 mm.

16 posteriorly. Nephridial papillae prominent, situated at anteroventral base of notopodia on segments 7–22. Holotype mature female, body wall distended with oocytes in mid and posterior segments; oocytes white, disc shaped, 120–180 µm in diameter.

Variation. Paratype material widest anteriorly, not inflated, occasionally with midposterior body coiled. Upper lip variably shaped, usually posteriorly deflected. Outer part of lower lip resembling subsequent midventral glandular pads, anterior edge developed as a flange; inner part of lower lip large, longitudinally grooved, inflated somewhat and extruding from mouth cavity. Eyespots faint, arranged in a broad transverse row, may be absent or faded. Branchiae on segments 2 and 3 about equal in size, posterior ones with slightly longer stalk up to a third of the total length of branchia.

Notopodia from segment 3, 28–34 pairs. Neuropodia from segment 5, arranged in double rows from segments 9–11 to pygidium; denticles arranged in 3–4 rows above rostrum as follows:—MF:3-4:4-7:9-15. Midventral pads extend from segment 2 to segments 14–16, first few always a yellowish colour. Nephridial papillae occur from segment 6 or 7 to segments 19–23.

Comment. *Neoleprea macrocercus* n. sp may be distinguished from all other species of *Neoleprea* in having 20 to 29 pairs of notopodia and eye spots present on the posterior tentacular lobe. It appears closest to *N. spiralis*, but differs in that the latter species has 38 pairs of notopodia and 20 to 22 midventral pads, whereas *N. macrocercus* has 28 to 34 pairs of notopodia and 13 to 15 pairs of midventral pads.

Etymology. Specific name derived from the greek *macro* and *kerkos*, tail referring to the long abdominal region.

Habitat. Occurs in reef areas intertidally to 20 m, underneath boulders and in crevices sometimes associated with coral and ascidians or encrusting algal turf.

Distribution. Victoria (Eagles Nest), New South Wales (South West Solitary Island, Minnie Water).

Nicolea Malmgren

Nicolea Malmgren, 1866: 380.—Hessle, 1917: 171.—Fauchald, 1977: 132.

Phyzelia Schmarda, 1861: 40.

Heterophyselia Quatrefages, 1865: 386.

Thelepella Chamberlin, 1919: 422.

Branchiae, 2 pairs, dichotomously branched. Lateral lobes absent. Notopodia from segment 4, 15–40 pairs; notosetae smooth tipped. Neuropodia with uncini from segment 5 (setiger 2), arranged in double rows on posterior thoracic segments.

Type species. *Terebella zostericola* Ørsted, 1844, designated by Malmgren, 1866.

Comments. The only species of *Nicolea* occurring in Australian waters according to Day & Hutchings (1977) was *N. bilobata* (Grube, 1877) recorded by Augener (1914), however as Day (1975) had earlier correctly pointed out, this species has lateral lobes on anterior segments and was referred to *Lanicides* by Hessle (1917). Other records of *Nicolea* from Australia include *N. venustula* Montagu, 1818 from Cockburn Sound, Western Australia (Day, 1975), *N. amnis* Hutchings & Murray, 1984 from Botany Bay, New South Wales and *N. minima* Hartmann-Schröder, 1984 from Albany, Western Australia. We have examined Day's specimens of *N. venustula*, and the paratype of *N. minima* and consider both to be synonymous with *N. amnis*. The description of *Nicolea amnis* was published in September 1984, and that of *N. minima* was published in November 1984, so that *N. amnis* has priority by two months. The material identified by Hartmann-Schröder (1979, 1980 and 1982) as *Nicolea venustula*, consists of *Pista violacea* Hartmann-Schröder 1984, and a species of *Lanicides*. Thus no records of *N. venustula* from Australia are valid. *Nicolea cetrata* was recorded from Western Port, Victoria, by Augener and omitted from Day & Hutchings (1979). It has been examined (ZMC) and referred to *Pista sinusa*, a new species described in this paper. A short discussion of the genus and its apparently conservative nature is given in Hutchings & Murray (1984).

Nicolea amnis Hutchings & Murray

Nicolea amnis Hutchings & Murray, (Sept.) 1984: 98–100, fig. 29.1–3.

Nicolea minima Hartmann-Schröder, (Nov.) 1984: 444–445, fig. 53.

Nicolea venustula.—Day, 1975: 201. *Non* Montagu, 1818.

Axionice harrisoni.—Knox & Cameron, 1971: 38. *Non* Benham, 1916.

Material examined. Western Australia: Cockburn Sound, 10(WAM 32-84); Bunbury 1(AM W203); Bussellton 2(NTM W2400); Torbay, Port Harding, near Migo Island 5(AM W200361), (AM W200360); 2 km off Cape Peron (AM W201041). South Australia: Great Australian Bight, 32°24'S, 133°30'E 2(AM W13626); Kangaroo Island, Emu Bay 5(AM W200582); Cape Northumberland 1(AM W200371). Tasmania: Tinderbox Bay 1(AM W200596); Maria Island, Darlington 1(AM W199251); Devonport, Horseshoe Reef 4(AM W200599). Bass Strait: Stn 139, 1(NMV F52599), Stn 199 1(NMV F52600). Victoria: Port Phillip Bay, Area 57, Stn 294, 1(NMV G1827), Area 56, Stn 295, 1(NMV G1828), Portland 3(NMV F52601); Gabo Island, south-south-east side 3(AM W200365), off Monumental Bay 2(AM W200368). New South Wales: Twofold Bay, Munganno Point 1(AM W200376), Quarantine Bay 1(AM W200378); Montague Island, 2(AM W200568); Botany Bay, HOLOTYPE (AM W196218), Port Jackson, North Head 3(AM W6397); Long Reef 2(AM W6973); Coffs Harbour 3(AM W200589); Minnie Water 1(AM W194967). Queensland: Caloundra 2(AM W200373); Capricorn Group, One Tree Island 1(AM W200381); Lizard Island,

between Bird and South (AM W200948). Northern Territory: Port Essington, Table Head 3 (NTM W1569); Darwin, East Point 2 (NTM W3046). A selection of material examined.

Comments. The material examined here greatly extends the distribution of this species, previously known only from New South Wales estuarine areas. This additional material also expands the variation occurring within the species. The size and degree of branchial branching increases with the size of the animal. Small individuals have two pairs of equal sized branchiae. Larger individuals have the first pair of branchiae considerably longer than the second pair. The number of pairs of notopodia also increases with size, ranging from 14 in small individuals to 17 in the largest specimens examined. The dental formula of the uncini is highly variable, both intraspecifically within a row and interspecifically as follows: MF:2-4:3-10. Nephridial papillae are present on segment 3, at the posterior base of the branchiae and on segments 6 and 7, they are situated at the dorsal base of the notopodia with the posterior two pairs larger, and often elongate.

In addition to the above variation, most of the material examined fell into one of two distinct size groupings, one group ranges from 0.7–1.4 mm in width, and the other from 2.2–7.0 mm in width. Both groups contained a proportion of sexually mature females and, apart from variations attributable to size, there appeared to be no other differences between the two size groups. It would appear, therefore, that *N. amnis* is a polytelic species, capable of reproducing at least twice during its life.

The holotype of *N. amnis* Hutchings & Murray (AM W198419) and the paratypes of *N. minima* Hartmann-Schröder (WAM 74-72), both fall into the small-size group, whereas the specimens identified by Day (1975) as *N. venustula*, (WAM 74-72), fall into the large-size group. These individuals show no additional variations or differences other than those listed here or by Hutchings & Murray (1984), and therefore *N. minima* is synonymised with *N. amnis* and the material identified by Day as *N. venustula* is referred to *N. amnis*.

We have examined material identified as *Axonice harrisoni* by Knox & Cameron (1971) from Port Phillip Bay (NMV G1828, G1827) and referred it to *Nicolea amnis*.

We have also examined the holotype of *Nicolea maxima* Augener, 1923 (HBM V9372) described from the Auckland Islands in the subantarctic. It is a very large species (20 cm in length and with a maximum width of 1 cm) and the arrangement of branchiae and the 20 pairs of notopodia clearly distinguishes it from *N. amnis*.

Habitat. Occurs in coastal and estuarine areas, from intertidal to 71 m. The species is associated with kelp holdfasts, clumps of tunicates, ascidians in colder waters, *Posidonia* seagrass beds and the algae *Caulerpa* and in coral substrate at One Tree Island.

Distribution. Widespread throughout Australian waters.

Phisidia Saint-Joseph

Phisidia Saint-Joseph, 1894: 167.

Branchiae absent; lateral lobes absent. Notopodia 14 pairs, beginning on segment 4. Notoetae distally denticulate; 2 types present, shorter coarser setae with pectinate appearance, longer setae fine and faintly denticulate. Neurosetae beginning on setiger 2, avicular.

Type species. *Leaena oculata* Langerhans, 1880 by monotypy.

Phisidia echuca n. sp.

Fig. 14a–d

Material examined. HOLOTYPE: South Australia: Kangaroo Island, Victor Harbour, 35°33'S, 138°38'E, just behind bluff, crevice fauna (AM W200472) 15 mm in length and 1.2 mm wide at anterior end. PARATYPES: 1(AHF Poly 1473), 1(USNM 99976), 1(BMNH ZB 1986.73), ranging in length from 12–15 mm in length and in width from 1–1.2; all paratypes gravid and USNM and BMNH material complete. All type material from same locality.

Additional material examined. South Australia: Streaky Bay, mud flats with *Posidonia* 1(AM W200474), 1(AM W200480) in amongst mussel clumps, several(AM W200475); Victor Harbour, Kangaroo Island, algal washings 1(AM W200476); Elliston reef, algae from reef flat at low tide 1(AM W200477), algal washings 2(AM W200481); southernmost tip of Murray River heads, underneath boulders covered in oysters and barnacles 1(AM W200478). Victoria: Port Phillip Bay, sand, 3 m 1(AM W16123); Western Port, Beacon Bottom Stn 312, 1(NMV F52602). New South Wales: Jervis Bay, Murrays Beach, *Zostera* seagrass beds 1(AM W194116), 1(AM W194171), 1(AM W194210), Botany Bay 1(AM W195552); Port Stephens, *Posidonia* seagrass beds 1(AM W12573), 1(AM W12459); South West Solitary Island 3(AM W200483).

Description. Complete individual with approximately 90 setigers. Preserved individual pale red in colour with patches of pale pigment especially marked on posterior abdomen. Gravid, coelom especially of abdominal segments heavily packed with oocytes.

Prostomium compact, with anteriorly directed ventral lip, with glandular margins. Prostomium dorsally flattened with thickened margins. Several grooved buccal tentacles remaining. Eye spots absent. Branchiae absent. Holotype punctured anteriorly, one nephridium protrudes mid-dorsally, adjacent to third notopodia. Nephridia are clearly visible in this position beneath thin epidermis in paratypes. Notopodia from segment 4, continue for 14 segments. Podia elongate flattened glandular structures (Fig. 14a). Notoetae arranged in 2 tiers, longest tier consisting of broad-bladed, narrow-

winged setae with elongated smooth tips; shorter tier, consisting of 2 types of setae, wingless capillaries with faintly serrated margins, tips of setae drawn out in fine point, broad-bladed, narrow-winged capillaries with smooth tips (Fig. 14b,c). Number of setae with faintly serrated margins increases posteriorly.

Neuropodia begin on segment 5 (setiger 2), continue to pygidium. Neuropodia well developed, especially on thorax where positioned on glandular tori, on abdomen, neuropodial tori erect, glandular. Neuropodial uncini initially arranged in single rows, arranged in double rows face to face on segments 11–20 (7th uncinigerous segment, to 3 segments beyond last pair of notopodia), following neuropodia with uncini arranged in single rows.

Neuropodial uncini avicular (Fig. 14d), with strongly crested head. Dental formula of uncini varying from MF:6:8: α : α , MF:7:10:12:15+ to MF:7:10: α . Well-developed discrete segmental ventral pads on segments 4–11, on following segments ventral pads rapidly decline in size, discrete midventral glandular stripe continues to pygidium. Pygidium small terminal rosette, with small papillae around margins.

Variation. One paratype shows evidence of regenerated posterior segments. The degree and extent of pigmentation of posterior segments varies. The BMNH specimen has U-shaped nephridia clearly visible through the epidermis of the dorsum between segments 6 and 9. The exact details of the nephridia are partially hidden by the numerous oocytes in the coelom in this region. Nephridial papillae are not visible.

The three paratypes exhibit variation in the degree of glandular development on the anterior segments ventrally. In some cases, the anterior ventral pads are raised and slightly paler in colour than the posterior ventral pads.

Additional material from Streaky Bay is considerably larger than the type series and the smooth-tipped setae appear faintly striated suggesting that the degree of serration may increase with size and presumably age. These differences are not considered sufficient to warrant referring the Streaky Bay material to another species. Eye spots are present on some large individuals.

The New South Wales material includes specimens with uncini arranged in double rows on segments 11–21.

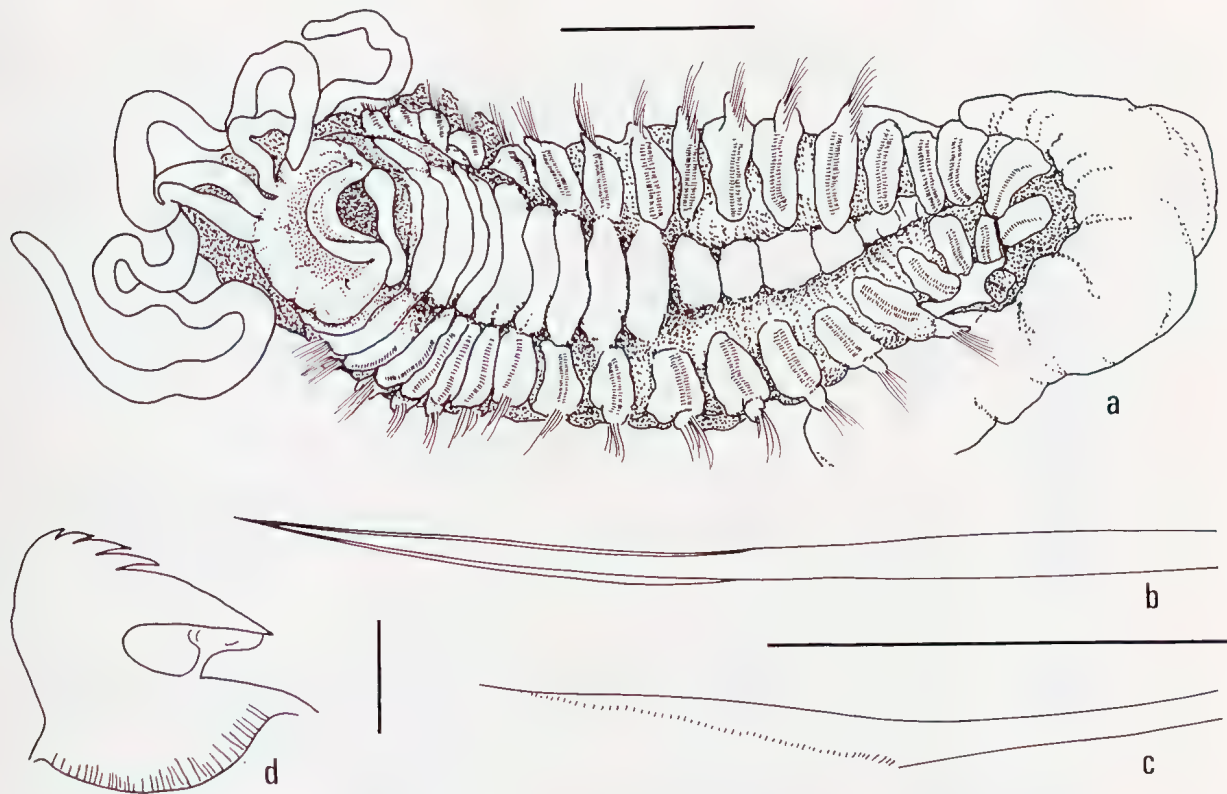


Fig. 14. *Phisidia echuca* n. sp., holotype. a. ventral view of anterior body, scale is 1 mm. b. long notoseta from thoracic setiger, scale is 0.1 mm. c. shorter notoseta from thoracic setiger, scale is 0.1 mm. d. uncinus from anterior thoracic setiger, scale is 0.01 mm.

Comments. Three species of *Phisidia* have previously been described: *P. aurea* Southward, 1956, *P. oculata* (Langerhans, 1880) and *P. sagamica* Hesse, 1917, all from the northern hemisphere. *Phisidia echuca* n. sp. can be distinguished from these three species by the segments on which the uncini are arranged in double rows, face to face, and the presence of strongly crested uncini. *Phisidia oculata* has 24 segments with double rows of uncini, *P. sagamica* has three segments with double rows of uncini. *Phisidia aurea* and *P. echuca* both have ten segments with uncini arranged in double rows. However, Southward (1956) indicates that the uncini of *P. aurea* have seven secondary teeth whereas uncini of *P. echuca* have at least four rows of teeth above the main fang with a large number of teeth in each row.

Etymology. The specific name *echuca* refers to an aboriginal name meaning a meeting of waters.

Habitat. Occurs intertidally and in shallow subtidal areas, often in mud with seagrass beds.

Distribution. South Australia, Victoria, New South Wales.

Pista Malmgren, emended

Pista Malmgren, 1866: 382.—Fauchald, 1977: 132.—Hutchings, 1977: 19.

Tentacular lobe compact, numerous buccal tentacles. Lateral lobes on segments 2–4; and sometimes on the peristomium. Branchiae, 1–3 pairs. Notopodia from segment 4, 17 pairs present; notosetae smooth-tipped, winged capillaries. Neurosetae begin on segment 5 (setiger 2) continue to pygidium. Uncini of anterior thoracic segments with posteriorly elongated bases, following uncini avicular, arranged in double rows on posterior thorax.

Type species. *Pista cristata* (O.F. Müller, 1776) by monotypy.

Comments. We have expanded the generic diagnosis of *Pista* to include species with well developed lateral lobes on the peristomium, and restricted the diagnosis to species with only 17 pairs of notopodia. Fauchald (1977) suggested that the numbers of notopodia may vary from 15 to 24. However we think that within the currently accepted species of *Pista*, several groups exist which perhaps should be separated into different genera. Species of *Pista* can be differentiated on the basis of the development and shape of the lateral lobes. To facilitate the differentiation of species of *Pista* present in Australia, the key diagnostic features have been tabulated in Table 1.

Table 1. Distinguishing features of Australian species of *Pista*.

Species	Peristomium	Presence and Shape of Lateral Lobes Seg 2	Seg 3	Seg 4	Nos. of branchiae	Type of branchiae	Thoracic segments with long handled uncini	Distribution
<i>P. australis</i>	thickened margins and ventrally forms a glandular V-shaped structure connected midventrally	semi-circular strong midventral connecting collar	semi-circular	small flattened semi-circular	2	plume shaped in spiral	5–11	south east Aust
<i>P. curtiuncata</i>	triangular blunt lobe connected midventrally by small medial lobe	small ventrally displaced semi-circular lobe	triangular-shaped lobe	narrow elongate lobe	2	plume shaped	all thoracic but weakly developed posteriorly	north west WA, NT
<i>P. pectinata</i>	large semi-circular lobe fused midventrally	only present as raised ridge across ventrum	large rectangular lobe	narrow rectangular lobe	3	long main stem with branches coming off along l axis	all thoracic	WA, Vict., NSW, Qld.
<i>P. sinusa</i>	large lateral semi-circular lobe connected midventrally	v. ventrally arranged lobe fused midventrally	bilobed lateral lobe fused to segment 2 forming sinus	narrow elongate lobe	2	short dichotomous branches	all thoracic	NSW, Qld. Vict.

<i>P. trina</i>	absent	ventrolateral lobe connected midventrally	flattened semi-circular lobe	no lobe — segment expanded across ventrum	3	richly dichotomous	5–11	Qld.
<i>P. trunca</i>	large rectangular lobe connected midventrally	small rounded ventrolateral lobe	large semi-circular lobe fused to segment 2 forming sinus	elongate rectangular lobe	2	sparsely dichotomous	all thoracic	Qld.
<i>P. turawa</i>	large lobes fused midventrally	absent	v. large semi-circular lobe expands ventrally to form connecting lobe	v. narrow elongate lobe	2	sparsely dichotomous	all thoracic	Continental slope off Sydney
<i>P. typha</i>	margins expanded forming 2 small lobes connected midventrally	small lobe connected midventrally	large semi-spherical lobe	small semi-spherical lobe	2	plume shaped in tiers	5–11	Qld.
<i>P. violacea</i>	large lateral lobe encompassing tentacles, connected midventrally	lateroventral lobe connected midventrally	large lateral lobe — connected mid-dorsally as a shelf	small rectangular lobe	2	sparsely dichotomous	5–8	all States except Qld.

Key to the Australian species of *Pista*

1. Branchiae with short branches along 1 side of main stem. *P. pectinata*
 —Branchiae plume shaped or with dichotomous branching. 2
2. Branchiae plume shaped. 3
 —Branchiae with dichotomous branching. 5
3. Margins of peristomium thickened but not forming a lateral lobe. *P. australis*
 —Margins of peristomium expanded to form a lateral lobe. 4
4. Segment 4 with narrow elongate lateral lobe. *P. curtiuncata*
 —Segment 4 with small semi-spherical lobe. *P. typha*
5. Sinus developed inside lateral lobe of segment 3. 6
 —Sinus absent inside lateral lobe of segment 3. 7
6. Segment 4 with lateral lobe which extends across the dorsum as a tripartite shelf. *P. sinusa*
 —Segment 4 with lateral lobe which extends across the dorsum as a straight shelf. *P. trunca*
7. Peristomium expanded to form a glandular lateral lobe. 8
 —Peristomium not expanded to form a glandular lateral lobe. *P. trina*
8. Segment 4 with narrow elongate lateral lobe not extending onto dorsum; body pale yellow in colour; branchiae with few branches. *P. turawa*
 —Segment 4 with small rectangular lateral lobe extends across dorsum as a shelf; body typically deep purple in colour; branchiae with numerous branches. ... *P. violacea*

Pista australis n. sp.

Fig. 15a-f

Pista typha.—Knox & Cameron, 1971: 38.—Hutchings, 1977: 22–23 (in part. rest = *P. typha*).—Hutchings & Rainer, 1979: 789–790.—Hutchings & Murray 1984: 100. *Non* Grube, 1878.

Material examined. HOLOTYPE: New South Wales: Merimbula 36°53'S, 149°52'E 1(AM W200877) *Zostera* and *Halophila*, complete 3.2 cm in length and 2.0 mm wide. PARATYPES: New South Wales: Merimbula 10(AM

W11773), 2(AM W11382), several(AM W11769), (USNM 99977); many(BMNH ZB 1986.74.91); many(AHF Poly 1474). All paratype material collected from *Posidonia* seagrass beds.

Additional material examined. South Australia: Streaky Bay 2(AM W200449): Upper Gulf, Stn Vincents, *Zostera* beds (AM W5977), (AM W 19380). Bass Strait: Stn 99 40°05.8'S, 143°17.5'E, 141 m (NMV F52605). Victoria: Port Phillip Bay, Stn 942 7 m, (NMV unreg), Stn 940 8 m, silty clay (NMV unreg), Western Port, Crib Point (NMV unreg), WP17077-1, (NMV unreg), WP1709-1 (NMV



Fig. 15. *Pista australis* n. sp., holotype. a. ventral view of anterior body, scale is 1 mm. b. lateral view of anterior body, scale is 1 mm. c. notoseta from thoracic setiger, scale is 0.1 mm. d. uncinus from 1st thoracic unciniger, scale is 0.01 mm. e. uncinus from 3rd thoracic unciniger, scale is 0.01 mm. f. uncinus from 7th thoracic unciniger, scale is 0.01 mm.

unreg), WP1739-2 (NMV unreg), WP1736-3 (NMV unreg), WBES Stn 1717 (NMV unreg), 1718 (NMV unreg), 1719 (NMV unreg), Gabo Island, 20 m (AM W201173). New South Wales: Merimbula (AM W11772), (AM W11777), (AM W11409), (AM W11765), (AM W11775), (AM W194082), (AM W194150), (AM W195752), (AM W194267), (AM W194429), (AM W194151), (AM W194209); Twofold Bay, Munganno Point 1 (AM W200635), 1 (AM W200637), Wallis Lake (AM W200347).

Description. Preserved body pale pink, complete. Buccal tentacles numerous arising from thickened glandular margin (Fig. 15a). Prostomium compact with anteriorly projecting tongue, glandular with convoluted margin (Fig. 15b). Eye spots absent. Peristomium thickened, on ventrum forms a glandular V-shaped structure connected midventrally.

Branchiae 2 pairs on segments 2 and 3, each pair consists of very unequal sized branchiae, largest on segment 2, followed by slightly smaller one on segment 3, smallest branchia occurs on segment 2. Stalk of branchia stout with marked annulations. Branchiae plume shaped with tufts of branched filaments coming off in spiral fashion around main stalk (Fig. 15a).

Branchiae developed from anterior margin of segments 2 and 3 (Fig. 15a) located considerably dorsal relative to where notopodia arise on segment 4.

Lateral lobes present on segments 2, 3 and 4. Segment 2 with flattened semi-circular lobe, dorsolateral in position with strong midventral connecting collar. Segment 3 with flattened semi-circular lobe more lateral in position than one present on segment 2, lobe connected across ventrum by a narrow ridge. Segment 4 with small flattened semi-circular lobe, more ventrally located than one present on segment 3, connected across ventrum by narrow ridge (Fig. 15b). Ventral glandular pads discrete from segment 5, occur on following 13 segments, then pads rapidly disappear, narrow midventral stripe continues for rest of thorax.

Notopodia from segment 4, continue for 17 segments. Notopodia globular rectangular, setae within bundle graded in length, longest setae occur dorsally. Notosetae arranged in 2 tiers, narrow winged, broad-bladed capillaries with long fine, smooth tips (Fig. 15c). Blades present only for distal quarter of setal length. Neuropodia from segment 5 (setiger 2), continue to pygidium, thoracic neuropodia long on flattened glandular tori, abdominal tori shorter, erect podia, last few abdominal tori extremely short. Uncini initially arranged in single rows, from seventh uncinigerous segment uncini arranged in double rows; this arrangement continues for rest of thorax, uncini arranged in single rows on abdominal tori. Uncini of first uncinigerous segment avicular with well-developed chitinised shaft (Fig. 15d). Uncinial shaft fragile and often breaks during preparation of slide

mount. If this happens base of uncinus can easily be seen as damaged where shaft was attached. Dental formula of uncini of first neuropodia MF:6-7:6:7-8; strongly crested head with teeth of second row well developed. Uncini of third uncinigerous row with shaft, but shaft more delicate than those found on first row of uncini (Fig. 15e). Uncini of fifth uncinigerous segment still with shaft, but less chitinised than those found on third uncinigerous segment. Dental formulae of uncini from fifth uncinigerous segment MF:6:7-8:6:α, teeth smaller than those found on first uncinigerous segment, number of teeth difficult to count as not arranged in regular rows. By seventh uncinigerous segment, shaft remains only as remnant, degenerating into connecting tendon (Fig. 15f).

Pygidium, terminal with spherical opening with smooth margins. No gametes visible in coelom. Prominent glandular, spherical nephridial papillae present on setigers 3 and 4; inserted inter-segmentally dorsally to notopodia.

Variation. The paratypes exhibit considerable variation in the amount of brown pigment present on anterior segments. Paratypes range in colour from pale cream to dark brown. Many have lost a branchia and considerable variation exists as to which branchia is the largest. The non type material also exhibits considerable variation in the development of the branchiae. Specimens vary in the development of the glandular area of the peristomium. Similarly the lateral lobe on segment 2 has variable amounts of glandular tissue present. A few specimens exhibit a reduction in size of notopodia posteriorly.

Comments. Hutchings (1977) discussed the species of *Pista*, which have two pairs of branchiae, and the ways in which these species could be separated. The only species of this complex occurring in Australia is *Pista typha*. *Pista australis* can be distinguished from *P. typha* by the shape of the peristomial fold (compare Figs. 15a,b; 17f) and by the shape of the uncini (see also Table 1).

The two species also appear to have different geographical distributions.

Etymology. The specific name *australis* refers to its wide spread distribution in south-eastern Australia.

Habitat. Occurs in sheltered estuaries or embayments, in seagrass beds.

Distribution. South Australia, Bass Strait, Victoria, New South Wales.

Pista curtiuncata Hartmann-Schröder

Fig. 16a

Pista curtiuncata Hartmann-Schröder, 1981: 58, figs. 134-136; 1985:86.

Material examined. HOLOTYPE: Western Australia: Cervantes (HBM P16500); Mangrove Bay, North West Cape 1 (WAM 13-84), 1 (WAM 11-84), 1 (WAM 16-84), Mermaid Sound, Dampier Archipelago 1 (WAM 23-84),

North West Shelf, Stn 03-83-B2G, 19°56.9'S, 117°52.8'E, several (AM W201202), Stn 05-83-B9G, 19°29.0'S, 118°55.2'E, several (AM W201200), Stn 01-83-B17G, 20°00.3'S, 117°00.4'E, 2 (AM W201191), Stn 04-83-B8G, 19°29.6'S, 118°52.2'E, 2 (AM W201192), Stn 06-82-B9G, 19°27.2'S, 118°58.4'E, 3 (AM W201201). A selection of material examined from North West Shelf, Northern Territory, Arafura Sea (8°09'S 134°50'E) 115 m (AM W200966). Queensland: Pallarenda Beach, North of Townsville (AM W18122); Calliope River 1 (AM W19175), 1 (AM W19176), 1 (AM W19177).

Comments. The following are based upon the holotype. The two pairs of branchiae have a strongly ridged thick main stalk, with the main branches coming off the central axis spirally. These main branches are themselves branched.

Peristomium with a triangular blunt lateral lobe, laterally displaced, connected midventrally by small medial lobe. Segment 2 with small ventrally displaced semi-circular lobe connected midventrally by a narrow pleated ridge. Segment 3 with a triangular shaped lateral lobe extending dorsolaterally and connected by a narrow shelf across the ventrum (Fig. 16a). The second pair of branchiae are attached to the anterior margin of segment 3 which is thickened and forms a dorsal ridge. Segment 4 with a small, narrow, elongate lateral lobe which merges with the ventral pads.

The non-type material resembles the holotype, although the material from North West Shelf is extremely small (1–2 mm in length) and much of the material is not in good condition.

Habitat. Occurs in intertidal seagrass beds and mud flats in front of mangroves and is also found at 115 m on the North West Shelf.

Distribution. Western Australia (North West), Northern Territory (Arafura Sea), Queensland.

Pista pectinata Hutchings

Pista pectinata Hutchings, 1977: 19–20, fig. 9a–g. — Hutchings & Murray, 1984: 100.

Pista cf. *pectinata*. — Hartmann-Schröder, 1983: 149.

Material examined. Western Australia: Dunsborough 1 (HZM P17613), North West Shelf Stn 03-83-B2G, 19°56.9'S, 117°52.8'E (AM W201187). Victoria: Western Port, WBES Stn 1717 (NMV F52604) CPBS Stn 12N, 2 (NMV F52609), CPBS Stn 015, 4 (NMV F52610), CPBS 03S, 1 (NMV F52611) Stn 1738 (NMV unreg). New South Wales: Hawkesbury River 1 (AM W19337). Queensland: Gladstone, Calliope River 1 (AM W10333), Auckland Creek 1 (AM W198256), (AM W198242), 1 (AM W198260), 1 (AM W198255).

Comments. This study has extended the range of *P. pectinata* which was previously only known from the east coast of Australia. Material identified by Hartmann-Schröder (1983) as *P. cf. pectinata* from Dunsborough in Western Australia (HZM P17613) has been examined and referred to *P. pectinata*. No other species of *Pista* has been described with this type of branchiae.

Since describing *P. pectinata*, it has become apparent that the arrangement of lateral lobes is one of the most important characters. Therefore, an expanded description of the lateral lobes of *P. pectinata* is given here. Peristomium with large semicircular lobe encompassing base of tentacles, resembling two wings, which are fused midventrally with a distinct notch, central connecting section not as glandular as two lateral wings. Segment 2 with virtually no development of lateral lobes but present as a connecting raised ridge across ventrum; segment 3 with large rectangular lobe connected midventrally by narrow strip; segment 4 with narrow rectangular lobe, lateral in position.

Habitat. Occurs in a variety of soft substrates ranging from silty sand to coarse gravel, in depths of 5–50 m.

Distribution. Western Australia (Dunsborough), Victoria (Western Port), New South Wales (Hawkesbury River), Queensland (Moreton Bay, Gladstone).

Pista sinusa n. sp.

Fig. 16b–e

Pista typha. — Knox & Cameron, 1971: 38. *Non* Grube, 1878.

Nicolaia cetrata. — Augener, 1927: 249–251. *Non* Ehlers, 1887.

Material examined. HOLOTYPE: Victoria: Western Port, Crib Point, Stn 31N 38°20.94'S, 145°13.62'E (NMV F52573) 2.5 cm in length and 2 mm in width anteriorly, but posteriorly incomplete with 32 setigers. PARATYPES: Port Phillip Bay, Stn 907 37°57.7'S, 144°44.7'E 1 (NMV F52579), Western Port, Crib Point, Stn 31N 1 (NMV F52574), Stn 32N 2 (AM W200767), Stn 32S 38°21'60", 145°13.67'E 1 (USNM 99978), 1 (BMNH ZB 1986.92), Stn 32N 1 (NMV F52575), 1 (NMV F52576), 32S 3 (NMV F52577), 3 (NMV F52578), Stn 22N 2 (NMV 52580), Stn 31N 2 (NMV 52581).

Additional material examined. Bass Strait, Stn 179 39°03.2'S, 146°39.5'E, 55 m (NMV F52605). Victoria: Port Phillip Bay, Area 28, Stn 286 (NMV G1717); Western Port (ZMC).

Description. Prostomium compact with several short grooved buccal tentacles remaining. Peristomium with large lateral semi-circular lobe connected midventrally by a U-shaped thickened ridge. Eye spots absent.

One branchia remaining on segment 2, mid-dorsal in position, branchial scars present on segment 3. Branchia short thick main trunk with several short dichotomous branches arising from the main stem.

Segment 2 with very, ventrally arranged lateral lobe, fused midventrally, dorsal margin of segment thickened and slightly raised from which first pair of branchiae arise. Segment 3 with bilobed lateral lobe fused midventrally as a narrow connecting strip, which forms a connecting ridge across the mid dorsum (Fig. 16b). On the inside of this lateral lobe, a

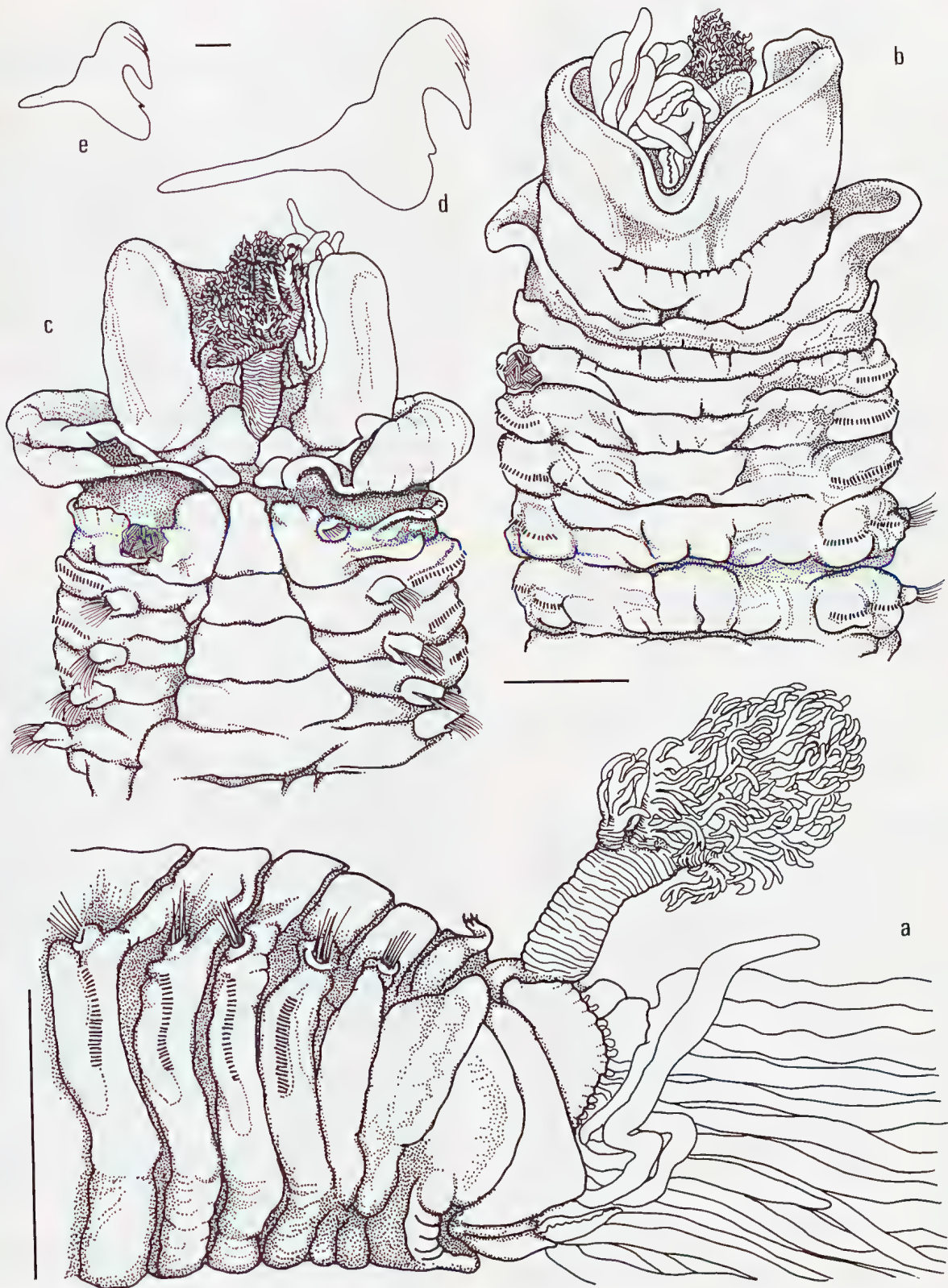


Fig.16. *Pista curtiuncata* holotype. a. ventrolateral view, anterior body, scale is 1 mm. *Pista sinusa* n. sp., holotype. b. ventral view, anterior body, scale is 1 mm. c. dorsal view, anterior body, scale is 1 mm. d. uncinus from 1st uncinigerous segment, scale is 0.01 mm. e. uncinus from 6th uncinigerous segment, scale is 0.01 mm.

connecting strip which is fused to segment 2 forming a blindly ending pocket or sinus (Fig. 16c). Segment 4 with small narrow elongate lateral lobe which connects onto the ventral pad, and connected across the dorsum by a tripartite shelf. Seventeen pairs of notopodia from segment 4, first pair of notopodia displaced towards mid-dorsal line, subsequent notopodia gradually realigned towards lateral position. Notosetae of 2 lengths, all broad-bladed, narrow-winged, smooth-tipped capillaries. Neuropodia from segment 5 (setiger 2) initially with uncini arranged in single rows, subsequently uncini in double rows from seventh uncinigerous segment to last thoracic segment, uncini arranged in single rows on abdominal tori. Uncini from first uncinigerous segment with well-chitinated long handled shafts and strongly crested heads with a dental formula MF:5-5-7: α : α , the last 2 rows each with numerous small teeth (Fig. 16d) which cannot be counted. Uncinial shaft is maintained on all thoracic uncini (Fig. 16e), the shaft still well developed on last thoracic uncinigerous segment. Abdominal uncini arranged on elongate rectangular tori with a small notopodial cirri; abdominal uncini lacking any shaft, all short-handled avicular uncini.

Ventral glandular pads present until setiger 14, then become less well differentiated and subsequently merge into a narrow midventral groove. Nephridial papillae not seen on holotype.

Variation. All the paratype material is incomplete and no specimen has a complete set of branchiae. The dentition of the thoracic uncini varies from MF:6:10: α : α to MF:6:8: α : α , with the teeth of the 1st row above the main fang long and pointed.

Comments. *Pista sinusa* most closely resembles *Pista trunca* Hutchings, 1977 in the development of a sinus inside the lateral lobe. This type of structure has not been reported from any other species of *Pista*. However it should be noted that in the original description of *P. trunca* the sinus was not detected.

Pista sinusa can be easily distinguished from *P. trunca* by the tripartite dorsal shelf connecting the lateral lobes of segment 4, whereas in *P. trunca* this shelf is not lobed. The dentition of the uncini and the development of the uncinial shaft along the thorax, also differs in the two species. *Pista sinusa* maintains an uncinial shaft to the last thoracic uncinigerous segment whereas in *P. trunca* the shaft has disappeared by the posterior thorax. To distinguish *P. sinusa* from other Australian species of *Pista* see Table 1.

Etymology. The specific name *sinusa* refers to the development of a sinus on the inside of the lateral lobe, and is derived from the latin *sinus* meaning pocket or recess.

Habitat. Occurs in sheltered protected areas and in deeper oceanic waters of Bass Strait.

Distribution. Bass Strait, Victoria (Western Port, Port Phillip Bay).

Pista trina Hutchings

Pista trina Hutchings, 1977: 21–22, fig. 11a–e.

Material examined. HOLOTYPE: Queensland: Moreton Bay (AM W6798). New South Wales: Merimbula 1 (AM W11778), 1 (AM W11004).

Comments. The following additional comments on the lateral lobes are given. Segment 2 with ventrolaterally situated lobe connected midventrally by a U-shaped glandular strip. Segment 3 with flattened semi-circular lateral lobe extending as a free lobe laterodorsally, base of lobe more glandular than margins, lobes connected midventrally by a triangular glandular area. Segment 4 with no lateral lobe, segment expanded across the ventrum. Peristomium without any lateral extension.

No additional material of this species was found during this study.

Habitat. Occurs subtidally in muddy substrates.

Distribution. New South Wales (Merimbula), Queensland (Moreton Bay).

Pista trunca Hutchings

Fig. 17a

Pista trunca Hutchings, 1977: 20–21, fig. 10a–f.

Material examined. HOLOTYPE: Queensland: Moreton Bay (AM W6793); Great Barrier Reef, Stn D16, 14°32.2'S, 144°53.4'E, 11 m, 1 (BMNH ZB 1986.256), 1 (BMNH ZB 1986.258), Stn 26, 16°14.1'S, 146°0.8'E, 22 m, 1 (BMNH ZB 1986.259–260), Stn D, 14°25.2'S, 144°47.9'E, 15 m (BMNH ZB 1986.257).

Comments. The additional material collected closely resembles the type material, however more information is given on the positioning of the lateral lobes. Peristomium with large rectangular-shaped lateral lobe connected midventrally by a U-shaped glandular connecting strip with areolated glandular margins. Segment 2 with a small rounded ventrolaterally placed lateral lobe connected across the mid-dorsum. Segment 3 with large semi-circular lateral lobe which continues across the ventrum as a narrow ridge, inside the lobe is a connecting strip to the margin of segment 2 forming a pocket or sinus. Lateral lobe of segment 3 ridged longitudinally and slightly pigmented. Lateral lobe of segment 2 arises ventrolaterally to this sinus. Segment 4 with an elongated rectangular lateral lobe connected to glandular ventral pads, and continues across the dorsum as a straight ridge (Fig. 17a). Two pairs of branchiae arising dorsolaterally from the anterior thickened margins of segments 2 and 3.

The development of the sinus was omitted from the original description but is clearly present on all the material.

Habitat. Occurs subtidally in mud and coralline sand.

Distribution. Queensland (Great Barrier Reef, Moreton Bay).

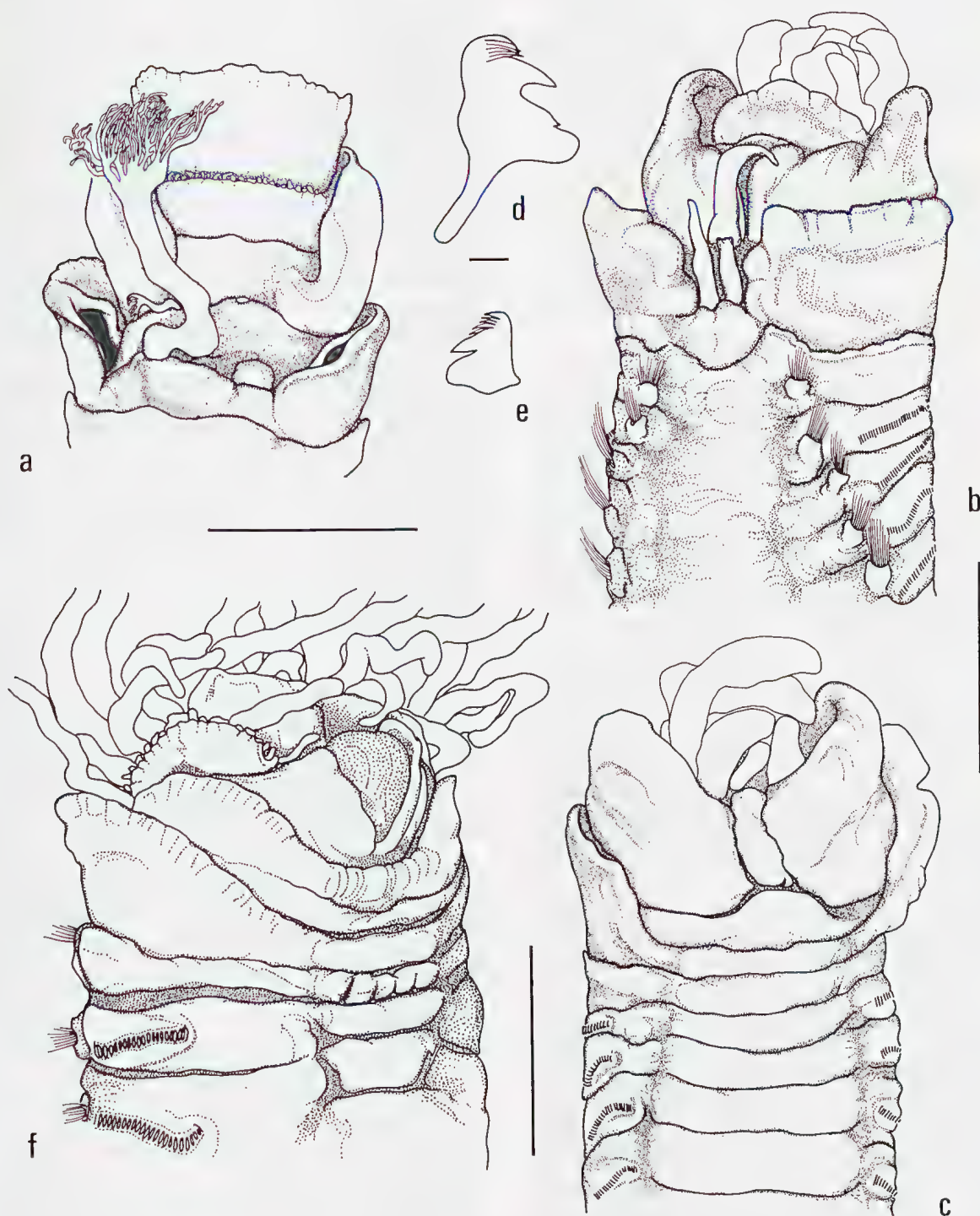


Fig. 17. *Pista trunca* holotype. a. dorsal view of anterior end showing sinus development of lateral lobe of segment 3, scale is 1 mm. *Pista turawa* n. sp., holotype. b. laterodorsal view of anterior body, scale is 1 mm. c. ventral view of anterior body, scale is 1 mm. d. uncinus from first thoracic uncinigerous segment, scale is 0.01 mm. e. uncinus from anterior abdominal segment, scale is 0.01 mm. *Pista typha* Royal Soc. Univ. of Qld. GBRE 1973 St. L4 coll. no. 158, 25.viii.73. f. lateroventral view of anterior end, scale is 1 mm.

Pista turawa n. sp.

Fig. 17b–e

Material examined. HOLOTYPE: (AM W200682) posteriorly incomplete, 2 cm long and 1.5 mm wide for 22 setigers. PARATYPES: several (AHF Poly 1475), several (BMNH ZB 1986.93–95), several (USNM 99979), many (AM W200683). All paratype material posteriorly incomplete. All material from the continental slope off Sydney, New South Wales, 34°16.1'S, 153°26.7'E, 4860–4866 m, collected by epibenthic sled.

Description. Alcohol preserved animal, pale yellow, posterior end not well preserved as found in thick muddy tube with pieces of foraminifera and sponge spicules embedded in walls.

Prostomium compact with numerous grooved buccal tentacles present. Eye spots absent. Branchiae, 2 pairs on segments 2 and 3, each branchiae with thin main stalk and 1 or 2 branches coming off.

Peristomium with very large inverted U-shaped lateral lobes fused midventrally with a wedge of glandular material. Segment 2 very narrow segment with no lateral lobe. Segment 3 with very large semi-circular lobe, very glandular at the base, extends as a lobe onto the laterodorsal margin, also expands ventrally to form a small ventromedial connecting lobe which connects the 2 lateral lobes together. Ventromedial lobe very glandular and thick. Segment 4 with very narrow elongate lateral lobe merges onto ventral glandular pads (Fig. 17b,c).

Seventeen pairs of notopodia beginning on segment 4. Notoetae golden yellow capillaries, all of similar length, broad-bladed, narrow-winged capillaries, drawn out into fine points. Neuropodia begin on segment 5 (setiger 2), thoracic uncini initially arranged in single rows, but arranged in double rows from the seventh uncinigerous thoracic segment, until the end of the thorax; uncini arranged in single rows in abdomen. Abdominal uncini on small rounded neuropodial pinnules projecting laterally towards the dorsum.

Uncini of first uncinigerous row with well developed chitinised shaft and a dental formula ranging from MF:3:6-8:8-10:α to MF: 3-4:6-8:8-10:α. Teeth in first row above main fang consist of a large central tooth and 1 smaller tooth on each side (Fig. 17d), or where 4 teeth occur, consist of 1 large tooth and 3 smaller ones. Uncinial shaft, well developed on all thoracic uncini. Dental formula of uncini from last thoracic uncinigerous segment MF: 3:4-5:6-8:α, with teeth in 1st row above main fang still unequal in size. Abdominal uncini lacking any shaft and with dental formula of MF:4-5:6-8:α:α (Fig. 17e), abdominal uncini considerably smaller than thoracic ones.

Initially ventral glandular pads rectangular and distinct for 1st, 9 setigers, following ventral pads develop a lateral glandular extension which merges with glandular area of the neuropodia. This arrangement continues for rest of thorax.

Last 2 or 3 thoracic segments bell-shaped with glandular girdles, subsequently the girdles continue

but following segments not elongated. Nephridial papillae not seen.

Variation. The paratypes vary considerably in their state of preservation, and they are easily damaged as the tubes are split open. The development of lateral lobes seems consistent, although there is some variation in the development of the branchiae.

Comments. *Pista turawa* n. sp. clearly differs from all the other Australian species of *Pista* in the development and arrangement of the lateral lobes, in the lack of a lateral lobe on segment 2 (see Table 1), and in the poorly developed branchiae. *Pista turawa* is unusual in the pronounced chitinised shaft on the uncini which is present throughout the thorax. The majority of *Pista* species have a chitinised shaft developed on only the first few thoracic segments, but in many species descriptions, the posterior thoracic uncini are not described, so perhaps this feature is more widespread than appears.

Several species of *Pista* from deep water have been described, *P. abyssicola* McIntosh, 1885, *P. corrientis* McIntosh, 1885, *P. disjuncta* Moore, 1923, *P. mirabilis* McIntosh, 1885, *P. vinogradovi* Uschakov, 1955 (= *P. pacifica* Uschakov, 1950, name preoccupied), *P. robustiseta* Caullery, 1944, *P. sibogae* Caullery, 1915, *P. sombreriana* McIntosh, 1885 and *P. vinogradovi* Uschakov, 1955 (transferred to the genus *Scionella*, see Holthe, 1986). Based on examination of McIntosh types and from the literature for the other species, *P. turawa* clearly differs from all these species in the limited development of the branchiae, the development of the lateral and peristomial lobe and the well-developed chitinised uncinial shaft present on all thoracic uncinigerous segments.

Etymology. The specific name *turawa* refers to the name of an Aboriginal tribe living on the coast just south of Sydney, the Turawal tribe.

Habitat. Occurs in deep water on the continental slope, living in dense colonies. A few of the tubes opened in the colony contained an ampharetid was present. It is very unusual to find these two families living in such close association.

Distribution. New South Wales (continental slope of Sydney).

Pista typha Grube

Fig. 17f

Terebella (Pista) typha Grube, 1878a: 232–233, pl. 12, fig. 4.

Pista typha.—Hutchings, 1977: 22–23, fig. 12a–b (in part. rest = *P. australis*).—Hutchings & Murray, 1984: 100 (in part. rest = *P. australis*). Non Hutchings & Rainer, 1979.

Material examined. HOLOTYPE: (MPW 518) Philippines (Bohol) Semper. Queensland: Great Barrier Reef: Stn D26, 16°41.1'S, 146°08'E, 22 m, (BMNH ZB 1986.124), Stn D16, 14°32.2'S, 144°53.4'E, 11 m, 1 (BMNH ZB 1986.130); Turtle Island, Stn K, 13°28.2'S, 143°42.0'E, 22 m, 5 (BMNH ZB 1986.128); Nymph Island Stn N6,

1(BMNH ZB 1986.158-160), Stn N1, 2(BMNH ZB 1986.126-127); Hope Island Stn EH 2, 3(BMNH ZB 1986.131-133); Low Isles, Stn L4, 16°23.2'S, 145°34.0'E, 4(BMNH ZB 1986.135-139), Stn L7, 1(BMNH ZB 1986.161-163), Stn L6, several(BMNH ZB 1986.154-157), Stn L2, 2(AM W200810), Stn L4, 5(AM W200811); Stn K5, 11°40.4'S, 143°58.3'E, 1(BMNH ZB 1986.128), Stn 2,4, 8(AM W200812), Three Isles Stn 3, 5(BMNH ZB 1986.146-151); Stn D32, 15°44.0'S, 145°27.1'E, 18 m, 1(BMNH ZB 1986.153), Stn D49, 14°42.6'S, 145°10.1'E, 1(BMNH ZB 1986.134) Stn D45, 15°37.3'S, 145°26.5'E, 18 m, 1(BMNH ZB 1986.164), Stn D34, 15°43.8'S, 145°29.2'E, 1(BMNH ZB 1986.125) Stn D5, 1(BMNH ZB 1986.152), Stn D41, 15°37.8'S 145°21.0'E, 1(BMNH ZB 1986.140); One Tree Island, lagoon (AM W201114). Calliope River, Gladstone (AM W198257), (AM W198258); 23°49'S 152°49'E, 348-357 m 1(AM W200964); Moreton Bay (AM W5053).

Holotype. The holotype of *P. typha* is a poorly preserved specimen in 2 pieces, total length 3 cm and 1.5 mm in width. The body wall is beginning to breakdown. The branchiae are tufted, plume like, with the branches coming off in a spiral, and each branch itself branched. Interpretation of the lateral lobes is a very tentative but appears that segment 3 has a laterally placed lobe and segment 4 has a small triangular lateral lobe adjacent to the notopodia. The holotype is damaged midventrally so it is not possible to see if the lateral lobes on segments 3 and 4 are connected midventrally. Peristomial folds are absent. The Queensland material agrees with the characters which can be determined on the holotype and an expanded description of *P. typha* based on the Australian material is given below.

Description. Two pairs of branchiae, first pair larger than second pair, branchiae of pair not equal in size. Considerable variation occurs as to which branchiae is largest, typically those on segment 2 are the largest, but it can be one of those occurring on segment 3. This suggests that *P. typha* can regenerate its branchiae if they are lost through predation.

Branchiae arise on anteriorly thickened projecting lip of anterior dorsal margin of segments 2 and 3. Branchial filaments come off main axis in tiers, individual filaments branched. Branching more pronounced on larger specimens. Eye spots present or absent.

Lateral lobes on segment 2 situated more laterally than those on segment 3, lobes connected midventrally, by distinct glandular strip. Larger lateral lobes on segment 3 than on segment 2. Lobes semi-spherical, more ventral than lobes on segment 2; base of lobe far more glandular than anterior margin, fuses ventrolaterally with ventral glandular pad. Segment 4 has small semi-spherical lobe, occurring very close to notopodia, continues across ventrum as thickened ridge which joins onto ventral glandular pad. Base of prostomium has thickened margin from which buccal tentacles arise and anteriorly projecting tongue. Margins of peristomium expanded, forming 2 small lobes connected midventrally by ridge (Fig. 17f) which forms an indented thickened ventral glandular strip.

Comments. Hutchings (1977) originally reported that *Pista typha* occurred from Moreton Bay in Queensland to Western Port and Port Phillip Bay in Victoria. Examining additional material revealed that two species had been confused as *P. typha*. *Pista typha* occurs in Queensland. South of Moreton Bay, Queensland, *P. australis* n. sp. occurs. The two species have similar branchiae but can be easily separated by the shape of the thoracic uncini and the development of the lateral lobe.

Habitat. Occurs from the intertidal to the continental slope (357 m) in muddy coral sand, living in compact tubes made of cemented sand grain.

Distribution. Queensland (Great Barrier Reef, Calliope River, Moreton Bay).

Pista violacea Hartmann-Schröder

Fig. 18a-b

Pista violacea Hartmann-Schröder, 1984: 45, figs 54-60.

Nicolea venustula.—Hartmann-Schröder, 1979: 148 (in part. rest = *Lanicides fascia*). *Non* Montagu, 1818.

Material examined. HOLOTYPE: Northern Territory: East Arm Boat Ramp, Darwin (NT W1644). Western Australia: Broome 1(HZM P16621), Halls Bank, Fremantle 10 m (AM W5490). PARATYPE: South Australia: Ceduna, Denial Bay 1(AM W198418) 1.2 m, intertidal in amongst algae; Upper Spencer Gulf, Chinaman's Creek 1(AM W5975); Maston, (AM W200899). Tasmania: D'Entree Casteaux Channel 43°2.42'S, 147°20.50E, 14.5-16.5 m, dredged (AM W200905). Bass Strait: Stn 107 (NMV F52606); Stn 117, (NMV F52607), Stn 219 (NMV F52608). New South Wales: Twofold Bay, Quarantine Bay 1(AM W200906), Jervis Bay, Darling Point 20 m 1(AM W200770), Split Solitary Island 1(AM W201318).

Description. The following additional information on the paratype and additional material collected is given. Paratype a small posteriorly incomplete specimen, about 1 cm in length, pale purple in colour. Only 1 branchia remains, having relatively long main stalk with few dichotomous branches. Branchiae or branchial scars situated on anterior margins of segments 2 and 3, almost on mid-dorsal line, in vertical arrangement. Prostomium compact. Peristomium with margins expanded to form large laterally encompassing lobes connected midventrally by inverted U-shaped connecting strip. Segment 2 with first pair of branchiae arising from thickened anterior margin which continues laterally as thickened margin, expands into lateroventral lobe, connects midventrally to form distinct collar, midsection pleated. Segment 3 with pair of large lateral lobes and connected across midventrum, bases of lateral lobes continue across mid-dorsum, to form shelf from which second pair of branchiae arise. Segment 4 with small rectangular lobe (Fig. 18a,b) not connected midventrally, forming ridge across dorsum. Arrangement of lateral lobes can be easily made out by tracing lobes from midventrum and gradually following them around to dorsum. First

pair of notopodia displaced dorsally in relation to subsequent notopodia. Abdominal neuropodia with small remnant notopodial cirri attached along edge of tori.

The additional material from southern Australia, which is much larger than Hartmann-Schröder's material, contains some material which have nephridial papillae on first and third setigers. The papillae are elongate and arranged intersegmentally

on the posterior margin of setigers 1 and 3. The specimens from the Bass Strait have varying amounts of the purple pigment present. The pigment appears to persist at least for several years in alcohol storage.

Comments. The distribution of *P. violacea* has been considerably expanded and Hutchings (in press) has recently found it in Hong Kong.

Habitat. Occurs from intertidal to depths of 43 m.

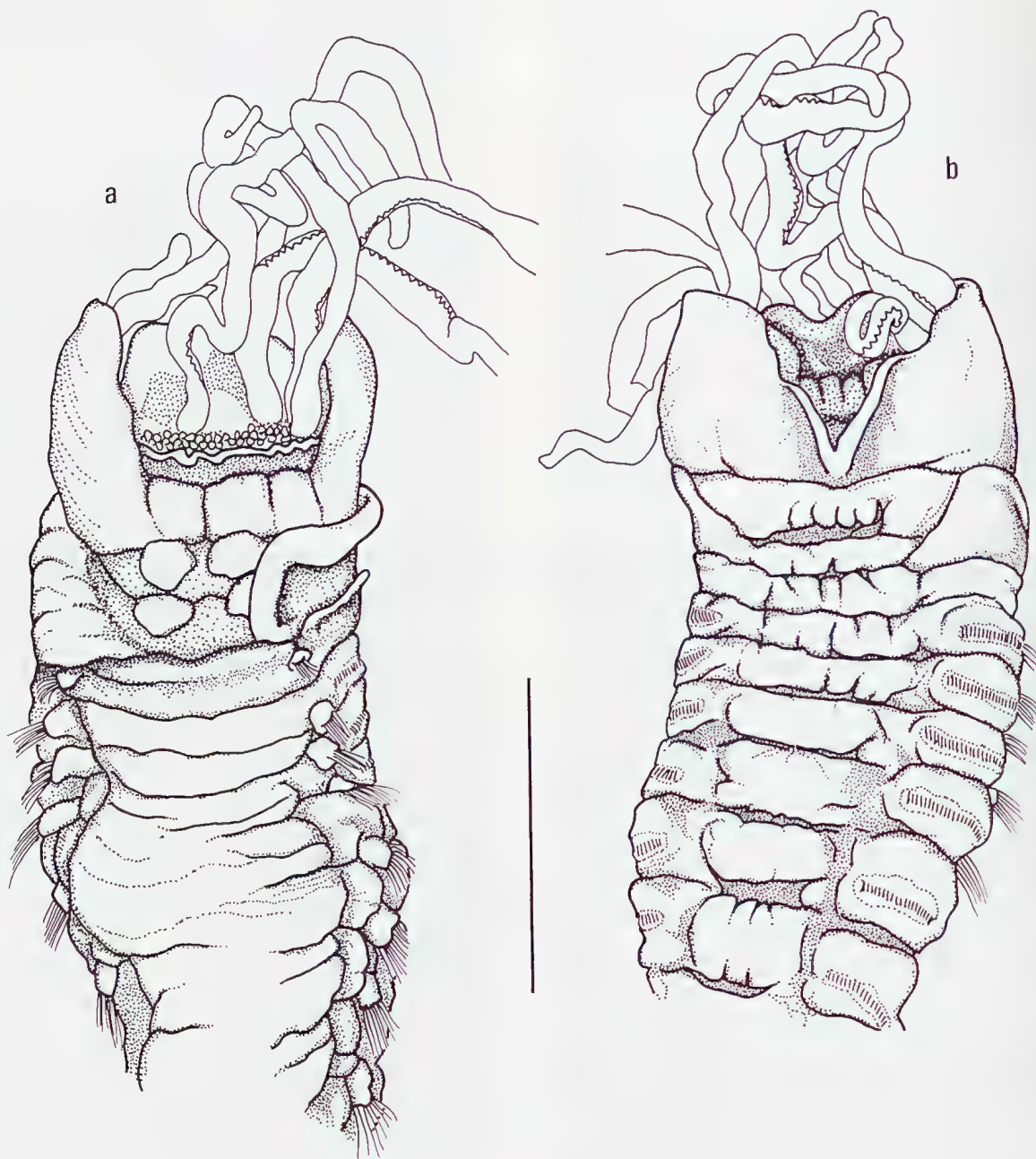


Fig.18. *Pista violacea* paratype (AM W198418). a. dorsal view of anterior body, scale is 1 mm. b. ventral view of anterior body, scale is 1 mm.

Distribution. Northern Territory, Western Australia, South Australia, Tasmania, Bass Strait, southern New South Wales.

Reteterebella Hartman, emended

Reteterebella Hartman, 1963: 355.

Branchiae, 3 pairs, on segments 2–4, stalked, dendritically branched. Lateral lobes inconspicuous or absent. Notopodia from segment 5, 16 pairs; notosetae smooth, narrowly winged capillaries. Neuropodia with uncini from segment 5 (setiger 2), arranged in single rows to segment 9, from segments 10–20 uncini arranged in double rows which alternate, face to face, abdominal uncini arranged in single rows. Abdominal uncini with fine tendons extending from base through each torus, these tendons absent on thoracic uncini. Nephridial papillae, 3 pairs on segments 3–5. Gonopores, 3 pairs on segments 6–8.

Type species. *Reteterebella queenslandia* Hartman, 1963, by original designation.

Comments. We have expanded the generic description of *Reteterebella* to include the absence of lateral lobes. Also the notopodia and neuropodia begin on the first post branchial segment as indicated by Hartman (1963), but we regard this as the fifth segment, not the fourth as stated by Hartman.

The presence of fine tendons in the abdominal tori resembles those of *Polycirrus* (Hutchings & Glasby, 1986b) and appears to be a relatively rare occurrence in the Amphitritinae. Rather than indicating any phylogenetic affinity with *Polycirrus*, however, we feel that this character is more likely to be an example of convergence as *Polycirrus* differs from *Reteterebella* in several major respects including the absence of branchiae and having uncini arranged in single rows throughout.

The genus was originally described from Australia, although Gibbs (1971) subsequently reported *R. queenslandia* from the Solomon Islands.

Key to the Australian species of *Reteterebella*

1. Lateral lobes absent; nephridial papilla on segment 5 dorsal to first pair of notopodia. *R. aloba*
- Lateral lobes present; nephridial papilla on segment 5 lateral to first pair of notopodia. *R. queenslandia*

***Reteterebella aloba* n. sp.**

Fig. 19a–g

Material examined. HOLOTYPE: New South Wales: Port Jackson, Bottle and Glass Rocks 35°53'S, 151°13'E (AM W200135); complete about 120 mm long, 99 segments, 9.0 mm wide. PARATYPES: Port Jackson 1 (AM W200134), Bottle and Glass Rocks 33°51'S, 151°16'E 3 (AM W102), Camp Cove 33°51'S, 151°17'E 1 (USNM 99980); Manly, Fairy Bower 30°53'S, 148°15'E 1 (AHF Poly 1476), 1 (BMNH ZB 1986.96). Paratypes range in width from 4.5–8.8 mm wide.

Additional material examined. South Australia: Kangaroo Island, Penneshaw Jetty 1 (AM W200136). New South Wales: Twofold Bay, Quarantine Bay 2 (AM W200138), Murrumbulga Point 1 (AM W200137).

Description. Body long, robust, widest midanteriorly, gradually tapering posteriorly. Tentacular lobe collar-like, prostomium short, smooth. Buccal tentacles absent. Eye spots faint, arranged in faint band across posterior tentacular lobe. Peristomium equal in length to segment 2 dorsally, slightly longer than segment 2 laterally, ventrally distinct, forming thin shelf-like lower lip, partially covering inner lips. Branchiae very prominent, 3 pairs, on segments 2–4, thickly stalked, heavily branched, first pair largest, succeeding pairs progressively smaller; arise just above line of notopodia. Lateral lobes absent (Fig. 19a).

Notopodia from segment 5, 16 pairs; podia rectangular with distal lobe enveloping notosetal bases (Fig. 19b). Notosetae smooth tipped, narrow-winged capillaries of 2 lengths, arranged in 2 tiers; surface of blade appears minutely pitted and granular, wings of setae faintly striated (Fig. 19c). Neurosetae from segment 5 (setiger 1), extending to pygidium; podia long, low ridges on thorax decreasing to about $\frac{1}{3}$ length of anterior segments, becoming elevated from body wall on first abdominal segment, then decreasing in length from midabdomen. Thoracic uncini with a delicate sub rostral guard visible under oil immersion and 2 rows of teeth surmounting a main fang, dental formula MF:1:1–4 with medial tooth largest in distal row (Fig. 19d,e); abdominal uncini without subrostral guard, *Polycirrus* like dental formula MF:1:2–4 (Fig. 19f,g). Uncini arranged in single rows to segment 9 and on abdominal segments, from segments 10–20 in double rows which alternate, face to face.

Midventral glandular pads extending to segment 16, thereafter a shallow glandular groove extending to pygidium; anteriorly, pads well developed, incised medially by a somewhat irregular furrow which extends to segment 10 or 11 (Fig. 19a). Three pairs of nephridial papillae on segments 3–5, first 2 pairs at posterolateral base of branchiae, 3rd pair just dorsal to first pair of notopodia, papillae small. Gonopores,



Fig.19. *Reteterebella aloba* n. sp., holotype. (AM W200135). a. lateroventral view of anterior body, scale is 1 mm. b. 5th notopodium from left side, anterior view, scale is 0.1 mm. c. long notoseta from setiger 5, scale is 0.1 mm. d. side view of uncinus from segment 10, scale is 0.01 mm. e-i. Frontal views of uncini from segment 10, scale is 0.01 mm. f. side view of uncinus from midabdominal setiger, scale is 0.01 mm. g-i. Frontal views of uncini from midabdominal setiger, scale is 0.01 mm.

3 pairs on segments 6–8, between noto- and neuropodia, represented by small, rounded swellings.

Variation. The paratype material exhibited the following variation: eyespots either faint or else heavily pigmented; lower lip shape variable, may be folded back revealing inner lips; structure of notosetae and uncini consistent with holotype, dental formula of uncini exhibiting slightly more variation than holotype with MF:1:1-8; midventral glandular pads without medial furrow in some specimens, variable; nephridial papillae and gonopores present on all specimens, but sometimes very small.

Comments. *Reteterebella aloba* n. sp. may be distinguished from *R. queenslandia* Hartman in lacking lateral lobes, in having the nephridial papillae on segment 5 dorsal to the first pair of notopodia rather than lateral to the first pair (Hartman, 1963, Fig. 1) and in the structure of the setae. Notosetae have a pitted surface in *Reteterebella aloba*, but have a smooth surface in *R. queenslandia*. The uncini change shape along the body in *Reteterebella aloba*, becoming *Polycirrus*-like on the abdomen but remain similar throughout in the Queensland species. In addition the dental formula of the uncini differs between the two species with *Reteterebella aloba* having one tooth in the first row above the main fang and *R. queenslandia* having at least two teeth in this position.

Etymology. The specific name *aloba* refers to the absence of lateral lobes, and is derived from the latin *lobus* meaning a rounded projection, like a lateral lobe and used in the negative.

Habitat. Occurs in sheltered marine waters 3–10 m, under rocks, or in crevices sometimes associated with sponge and *Posidonia* beds.

Distribution. South Australia (Penneshaw Jetty), New South Wales (Sydney region).

***Reteterebella queenslandia* Hartman**

Fig. 20a–d

Reteterebella queenslandia Hartman, 1963: 355–357, pl. 1, figs 1–3.—Gibbs, 1971: 198.

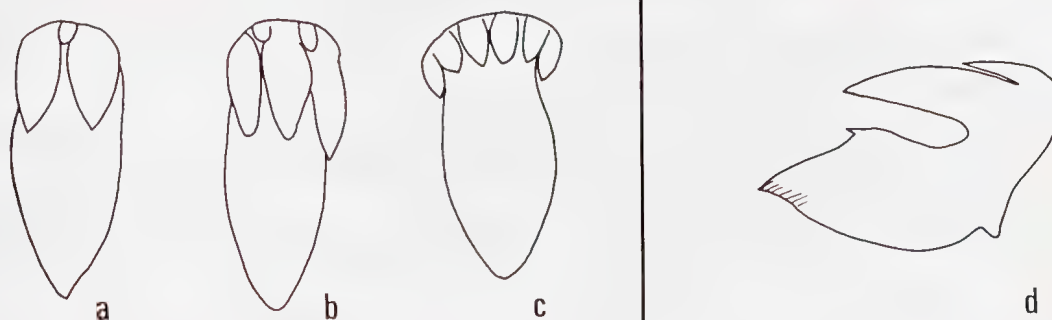


Fig. 20. *Reteterebella queenslandia* (AM W843). a. uncinus from segment 10, MF:2:1, scale is 0.05 mm. b. uncinus from segment 10, MF:3:2, scale is 0.05 mm. c. uncinus from segment 10, MF:6, scale is 0.05 mm. d. side view of uncinus from segment 10, scale is 0.05 mm.

Material examined. HOLOTYPE: Queensland: Heron Island, reef flat (AM W3755); Marian Reef, Coral Sea (AM W12421); Port Denison 1 (AM W843); Lizard Island, Coconut Beach 2 (AM W200132). Solomon Islands, Maraunibina Island (BMNH 1970.789).

Comments. The Lizard Island material examined shows no further variation than indicated by Hartman (1963). The specimen from Port Denison shows a greater range in the dental formula of uncini as follows:—MF:2-6:0-5 (Fig. 20a–c) but teeth in the distal row are minute and in side view the uncinus appears to have only one row surmounting the main fang as in the holotype (Fig. 20d). Material identified by Gibbs (1971) from the Solomon Islands has been re-examined and agrees closely with the type material from Australia.

The species probably occurs in north-west Australia, but no complete animals have been collected.

Habitat. Occurs on sandier parts of reef flat, usually under dead coral bounders also from 8 m at Lizard Island on fringing reef, in all cases animal deeply embedded in the reef, living in a soft, flimsy tube made of silt particles. Presence of worm indicated by long white tentacles extended for 1–2 m from animal; tentacles only partially retractile. Species may be locally abundant.

Distribution. Queensland.

***Terebella* Linnaeus, emended**

Terebella Linnaeus, 1767: 1092.—Hessle, 1917: 187.—

Fauvel, 1927: 254.—Day, 1967: 747.

Heteroterebella Quatrefages, 1865: 384.

Heterophyselia Quatrefages, 1865: 386.

Leprea Malmgren, 1866: 389.

Three pairs of branched branchiae from segment 2. Lateral lobes absent. Notopodia from segment 4, continue for a variable number of segments; notosetae distally serrated. Neuropodia with uncini from segment 5, arranged in double rows, face to face or alternate rows on posterior thorax. Nephridial papillae from segment 3.

Type species. *Terebella lapidaria* Linnaeus, 1767, by monotypy.

Comments. We have restricted the generic diagnosis of *Terebella* slightly to include only those species with three pairs of branched branchiae. Previous generic diagnoses (Fauvel, 1927; Day, 1967) have stated that two or three pairs of branchiae may be present. This, however, created some confusion as *Amphitritides* Augener, 1922 also has two pairs of branchiae and in other respects is indistinguishable from *Terebella*.

A literature review of all *Terebella* species listed by Hartman, 1959 (excluding questionable species) showed that almost all have three pairs of branched branchiae. The exceptions are *T. parvabranhiata* Treadwell, 1906 which apparently has only one pair, however Treadwell mentions that the animal was in poor condition and that other branchiae may have been lost; *T. pterochaeta* Schmarda, 1861, which has three pairs according to Schmarda but only two according to some later reports (McIntosh, 1885; Day, 1967); and *Terebella (Schmardanella) californica* Moore, 1904 which has two pairs of branchiae and has been transferred to *Neoleprea* by Banse, 1980.

Although we recognise the number of pairs of branchiae to be consistent within this genus, we have deliberately not specified the segments on which these occur. Most species of *Terebella* have branchiae on segments 2, 3 and 4, however a few species have the third pair of branchiae differently situated. For example *T. gorgonae* Monro, 1933 (BMNH 1933.7.10 286-290 and BMNH 1933.7.10.291-293) and *T. tantabiddycreekensis*, Hartmann-Schröder, 1980 have the third pair arising from the junction of segments 4 and 5, *T. ehrenbergi yappensis* Okuda, 1937 has the third pair arising from segment 5, *T. maculata* n. sp., this paper, has the third pair arising from segment 6 and *T. inversa* (Willey, 1905) has the third pair from segment 6 or 7. *Terebella haplochaeta* (Ehlers, 1904) has the third pair of branchiae arising from the posterior section of segment 4. The third

pair of branchiae in all these species is dorsally displaced. Other species of *Terebella* having the third pair of branchiae dorsally/posteriorly displaced may be found if type material was to be re-examined.

We have retained these aberrant species in the genus *Terebella* as they resemble other species of *Terebella* in other respects. Four species of *Terebella* are represented in Australian waters. *Terebella stenotaenia* Grube, 1871 was described from Moreton Bay, Queensland, however the description is very brief and the type material could not be located. *Terebella pappus* is common in southern waters, *T. tantabiddycreekensis* Hartmann-Schröder, 1980 is more common in northern waters, and *T. maculata* is known from a single record from the Lacepede Group, Western Australia. *Terebella haplochaeta* (Ehlers, 1904), originally described from New Zealand, has been widely recorded in Australia by Augener (1913, 1914) and Hartmann-Schröder (1980, 1981, 1983, 1984, 1985). Examination of the material described as *T. haplochaeta* from Australia indicated it is *Terebella tantabiddycreekensis* Hartmann-Schröder, 1980. The type (HZM PE 1188) of *Terebella haplochaeta* (Ehlers, 1904) has three pairs of branchiae on segments 2, 3 and 4 of which the second pair is inserted more laterally than those on segments 2 and 4. The first pair of branchiae arise at the junction of segments 2 and 3, second pair at the junction of segments 3 and 4, and the third pair arises in the middle of segment 4. The branchiae have a short thick main stalk with numerous dichotomous branches which come off along the main axis in a slightly spiralled fashion. The notosetae each have a distinct swelling at the base of the serrated blade. *Terebella haplochaeta* does not occur in Australia, and is restricted to subantarctic islands such as Auckland and Campbell Islands and New Zealand (Augener 1923, 1926, 1932; Benham 1927, 1950; Knox & Cameron 1970). Hartmann-Schröder (1979) also recorded *Terebella pterochaeta* Schmarda, 1861 from North West Australia and is synonymised with *Amphitritides ithya*, a new species described in this paper.

Key to the Australian species of *Terebella* *

1. Third pair of branchiae arises on segment 4. *T. pappus*
 — Third pair of branchiae arises elsewhere. 2
2. Third pair of branchiae arises on segment 6. *T. maculata*
 — Third pair of branchiae arises on the junction of segments 4 and 5.
 *T. tantabiddycreekensis*

* *Terebella stenotaenia* Grube is not included in the key as it is incompletely known.

Terebella maculata n. sp.

Fig. 21a–h

Material examined. HOLOTYPE: Western Australia, Lacepede Group, West Island 16°52'S, 122°08'E (WAM 26-84), complete, about 106 segments, 32 mm long, 2.3 mm wide, female.

Description. Body wall of midsection distended with eggs, abdomen gradually tapering, adorned with dark pigment spots on dorsum (Fig. 21a). Tentacular lobe compact. Buccal tentacles filiform, grooved, longest extending about half way back along body. Eyespots present in discontinuous band across posterior tentacular lobe, most numerous laterally, absent medially. Peristomium very short dorsally, equal in length to segment 2 laterally, forming broad, crescent-shaped lower lip ventrally. Branchiae richly branched, thick stalk, 3 pairs on segments 2, 3, 6; first two pairs arise just above line of notopodia, third pair dorsally displaced, slightly larger than first 2 pairs. Lateral lobes absent (Fig. 21b).

Notopodia from segment 4, continuing to near pygidium; podia slender, short initially (Fig. 21c), and reducing in size posteriorly to small tubercle. Notoetae in anterior notopodia of 2 lengths, arranged in 2 tiers, long, slender, narrow-winged capillaries with short, faintly hispid tip, and shorter setae of the same type (Fig. 21d,e); posteriorly notosetae with longer, broader hispid blade and narrow, wingless stem, graded lengths (Fig. 21f,g). Neuropodia from segment 5 (setiger 2), present on all subsequent segments to the pygidium; podia low ridges throughout, longest midanteriorly, decreasing in length gradually posteriorly. Uncini with small, anteriorly pointing, subrostral ligament (Fig. 21h), dental formula MF:3-4:5-8:α, similar throughout; uncini arranged in single rows to segment 10, then in double rows, face to face, last 25 or so segments uncini again arranged in single rows.

Midventral glandular pads on segments 2–13, thereafter a shallow, segmented, glandular groove to pygidium. Nephridial papillae large, 1 pair on segment 3, arising anterior to second pair of branchiae. Pygidium without anal cirri.

Comments. *Terebella maculata* n. sp. belongs to the group of *Terebella* which have the third pair of branchiae dorsally displaced and arising from segments 5 to 7. It differs from all of these in having uncini with a subrostral ligament. In addition it differs from the Australian species, *T. tantabiddycreekensis* in the dental formula of the uncini and the segment on which the third pair of branchiae arise.

Etymology. Specific name derived from the latin *macula* spot, (f), referring to the dark pigment spots adorning the abdomen.

Habitat. Occurs under rocks and in sandy mud intertidally.

Distributions. Western Australia (Lacepede Group).

Terebella pappus Hutchings & Murray

Fig. 22a–d

Terebella pappus Hutchings & Murray, 1984: 100–101, fig. 30.1–2.

Material examined. Western Australia: Nornalup 1(AM W200029). South Australia: Venus Bay 2(AM W200000); Coffin Bay 5(AM W199986); Daly Heads 2(AM W199981); Kangaroo Island, Cape du Couedic 5(AM W199985), American River 10(AM W199979); Coobowie 2(AM W18466); Port Augusta 4(AM W200004); Torrens Island 3(AM W6772); Port Gawler 1(AM W18468); Victor Harbour 3(AM W200006); Cape Dombey 1(AM W200005). Tasmania: Flinders Island, Lady Barron 2(AM W200030). Victoria: Western Port Stn 226, 3(NMV unreg); East of Grey River, Otway's Coast 6(AM W200027); Bastion Point 16(AM W200020); Gabo Island many (AM W200028). New South Wales: Lake Merimbula 1(AM W200037), HOLOTYPE (AM W196195), PARATYPES 17 (AM 196196); Green Cape 1(AM W200035); Twofold Bay, Munganno Point 15(AM W200008); O'Hara Heads, south of Ulladulla 4(AM W200039); Wreck Bay, Cemetery Point 5(AM W200036); Bellambi Beach, north of Wollongong 7(AM W200038); Long Reef 3(AM W200041); Lord Howe Island 2(AM W200042); Coffs Harbour 2(AM W200011); Minnie Water 20 (AM W200015); Ballina 4(AM W200018); Lennox Head 6(AM W200013). Queensland: Hervey Bay, Pinalba 9(AM W200019). A selection of material examined, size ranging from individuals with 48 segments, 4.6 mm long, 0.9 mm wide to individuals with 85 segments, 26 mm long, and 2.5 mm wide.

Comments. The holotype and paratypes were examined and compared to the present material. In the type material we found notosetae to consist of one type, varying in length viz. very narrow winged capillaries with the distal portion finely serrated (Fig. 20a). The uncini of a paratype specimen were as described by Hutchings & Murray, 1984 (Fig. 20b,c) with a dental formula MF:3-5:6-8.

The present material varies from the type material as follows: – branchiae all uniform in size or decreasing in size posteriorly; uncini with teeth arranged in two or three rows above a main fang as follows:–MF:3-7:6-13, uncini arranged in an alternate row from segment 7, either face to face or back to back, nephridial papillae on segment 2 or anterior edge of segment 3, plus up to four pairs of low nephridial papillae on segments 6 to 9, situated between notopodia and neuropodia although these posterior papillae are often absent.

Some specimens of *Terebella pappus* from Western Port had parasitic copepods attached to them (Fig. 22d). A similar structure was reported by Hutchings & Glasby (1986b) as occurring on the tentacular membrane of the polycirrinid *Amaeana trilobata*, but wrongly interpreted as an egg sac rather than a parasitic copepod.

Habitat. Occurs intertidally on rock platforms in crevices, under stones, boulders, in soft sediment in rock pools; associated with *Mytilus edulis*, coralline algae and the serpulid *Galeolaria*. Occasionally the species is found among mangroves.

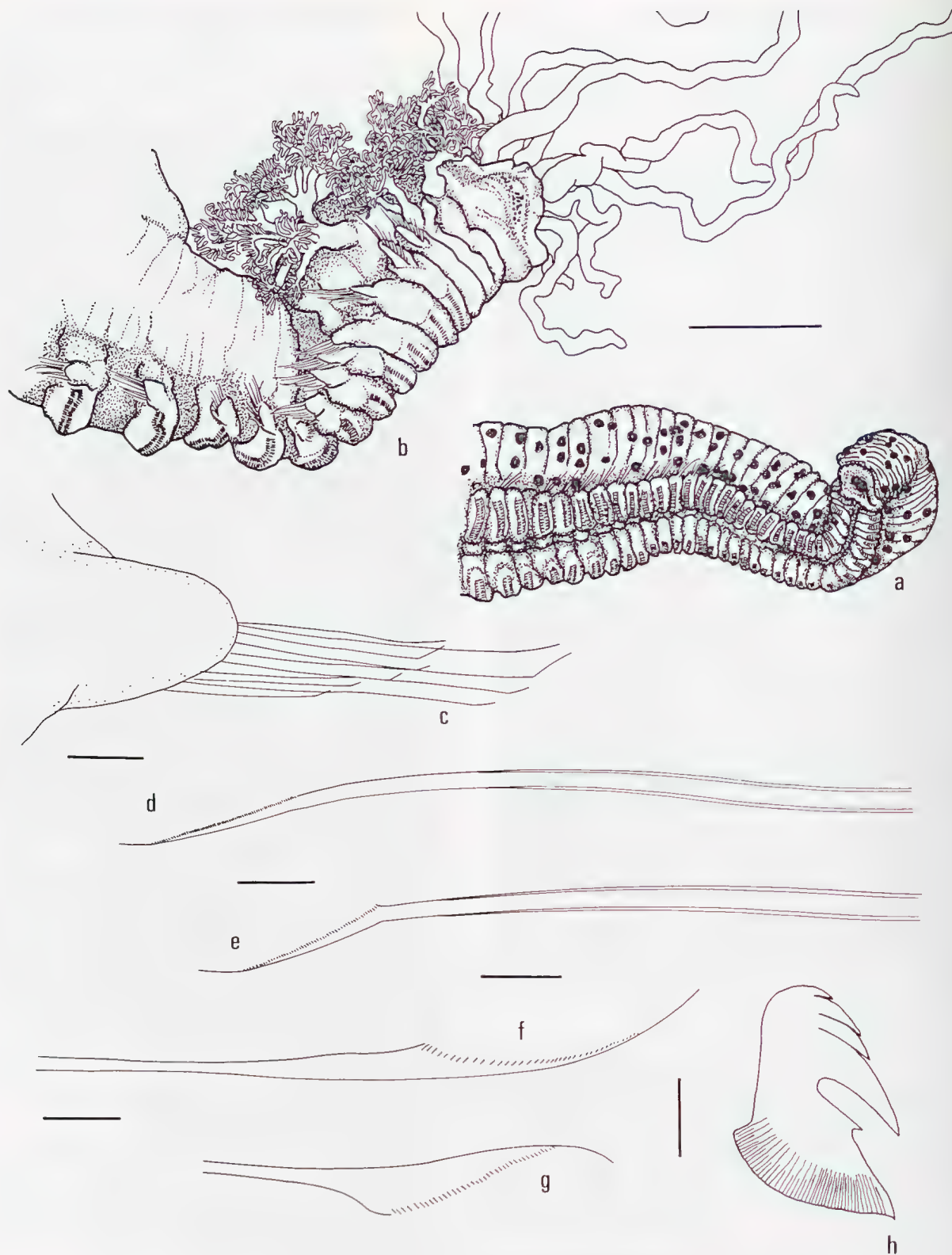


Fig.21. *Terebella maculata* n. sp., holotype. **a.** posterior end of body, ventral view, scale is 1 mm. **b.** anterior end of body, lateral view, scale is 1 mm. **c.** notopodia 4, left side (anterior) view, scale is 0.1 mm. **d.** long notoseta from notopodia 4, scale is 0.01 mm. **e.** shorter notoseta from notopodia 4, scale is 0.01 mm. **f.** long notoseta from midabdominal notopodium, scale is 0.01 mm. **g.** shorter notoseta from midabdominal notopodium, scale is 0.01 mm. **h.** uncinus from midabdominal segment, scale is 0.01 mm.

Distribution. Widespread and locally abundant in southern Australian waters.

Terebella stenotaenia Grube

Terebella stenotaenia Grube, 1871: 49.

Material examined. None.

Description. Based on the limited description given by Grube. Body with 34 segments. Branchiae, 3 pairs, dendritically branched. Notopodia from segment 4, present on all subsequent segments.

Comments. Type material has not been located. At this stage, it is unclear if this species even belongs to the genus *Terebella*.

Habitat. Unknown.

Distribution. Queensland (Moreton Bay).

Terebella tantabiddycreekensis Hartmann-Schröder

Terebella tantabiddycreekensis Hartmann-Schröder, 1980: 77–78, figs 122–123.

Terebella haplochaeta.—Hartmann-Schröder, 1980: 77 (?in part); ?1981: 58; ?1982: 91; ?1983: 149; 1984 (?in part only = at least 1 specimen of *Terebellas pappus*): 45; ?1985: 86; ?1986: 59.

Leprea haplochaeta.—Augener, 1913: 299–300; 1914: 87–89 (in part only, rest = ciratulid, maldanid and *Thelepus plagiostoma*).

Material examined. Western Australia: Exmouth (HBM P16623); Broome, Cable Beach 2(NTM W2147); Abrolhos Group, Rat Island 10(AM W200064), Shark Bay (HBM V8261); Cockburn Sound, Woodmans Point 2(WAM 51–87), Princess Royal Harbour (HBM V8262); Rottnest Island (HBM V8260). New South Wales: Jervis Bay, Green Point 3(AM W200119), off Moona Moona Creek 6(AM W200126); Bass Point 9(AM W200118); Clovelly 3(AM

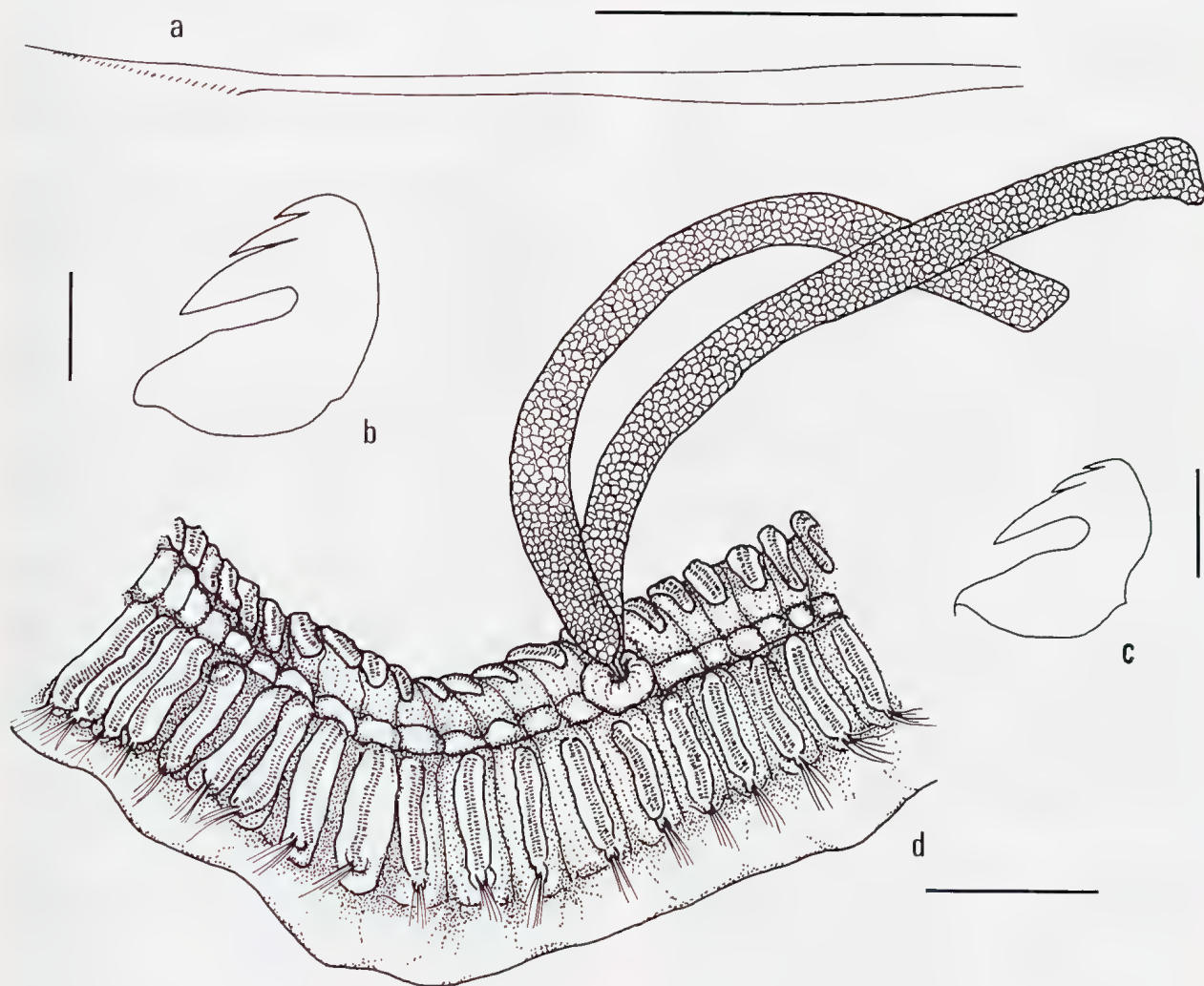


Fig. 22. *Terebella pappus* paratype (AM W196196). a. notoseta from setiger 6, scale is 0.1 mm. b. uncinus from setiger 13, scale is 0.01 mm. c. uncinus from setiger 50, scale is 0.01 mm. *Terebella pappus* NMV Survey 69/01–69/07 226, 5/1/69. d. ventral view, midabdominal setigers, with parasitic copepod, scale is 1 mm.

W200117); Long Reef 1(AM W200121); Terrigal Haven 5(AM W200130); Broughton Island 1(AM W13067); Lord Howe Island 3(AM W200108); South West Solitary Island 1(AM W200127); Minnie Water 1(AM W200112); Angourie Point 6(AM W200109). Queensland: Caloundra 1(AM W200061); Great Barrier Reef, One Tree Island 2(AM W200056), 1(AM W200055), 1(AM W200410), Lizard Island 1(AM W200075), 1(AM W200076), 4(AM W200068). Northern Territory: Fannie Bay 1(AM W200065). A selection of material examined, size range 73 segments, 11.2 mm long, 1.1 mm wide to 123 segments, 58 mm long, 5.2 mm wide.

Comments. The present records greatly extend the distribution of this species which was previously only known from Exmouth, Western Australia. The material examined showed the following variations: buccal tentacles with or without eyespots in preserved material; nephridial papillae on segments 3, 5 to 8 or 6 to 8 or 6 to 7, first pair elongate, cylindrical with diameter greatly expanded in one specimen from Bass Point, remaining pairs low, papilliform; notopodia extend for about two thirds to four fifths along body; notosetae of two lengths, shorter type with a subdistal swelling occasionally not as pronounced as illustrated by Hartmann-Schröder, 1980; uncini with dental formula MF:3:4-8, with most distal row containing teeth of variable size, some very small.

Terebella tantabiddycreekensis differs from other species of *Terebella* in having three pairs of richly branched gills, with the second pair laterally displaced and the third pair more dorsal, arising from the border of fourth and fifth segments; prominent nephridial papillae on segment 3, located anterodorsal to second pair of branchiae, plus low papillae, typically on segments 5 to 8 located ventral to notopodia; and two types of notosetae with shorter ones flagged, having a rounded, subdistal swelling below a serrated blade.

Material identified by Augener (1913, 1914) from Western Australia is in most cases referred to *T. tantabiddycreekensis* but a sample from Stn 64 on Rottnest Island is a mixture, consisting of a specimen of a cirratulid, a maldanid, *Thelepus plagiostoma* and *T. tantabiddycreekensis*. Hartmann-Schröder (1980, 1981, 1982, 1983, 1984, 1985, 1986) has recorded *T. haplochaeta* from many areas in Western Australia and South Australia. Some of this material has been examined. The material from Exmouth (HZM P16623) is *T. tantabiddycreekensis* but the specimen from Ceduna (HZM P18108) is *Terebella pappus*.

Habitat. Occurs intertidally to depths of 20 m often in reef environments, either rock or coral, associated with the kelp *Ecklonia radiata*, coralline algae, seagrass, Vermetidae and algal mats; sometimes associated with *Posidonia* seagrass beds.

Distribution. Australia, widespread north of about 32°S on the west coast and about 35°S on the east coast.

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Classification of Australian Bulniform Planorbids (Mollusca: Pulmonata)

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ABSTRACT. The genera of Australian bulniform planorbids have been examined anatomically and their classification reviewed. The major conclusions reached are: 1. *Isidorella* is not congeneric with *Bulinus* and is an endemic Australian genus; 2. Iredale's genera *Lenameria*, *Tasmadora* and *Mutalena* are synonyms of *Physastra* Tapparone-Canefri which, in turn, is a synonym of *Glyptophysa* Crosse. *Glyptamoda* Iredale is also a synonym of *Glyptophysa*; 3. *Oppletora* Iredale, synonymised with *Bulinus* by Hubendick, is actually related to *Glyptophysa* and is placed in a separate subgenus; 4. *Ancylastrum* Bourguignat has been examined and the results confirm Hubendick's opinion that this limpet-like genus is related to *Glyptophysa*. Two species can be separated by simple anatomical characters; 5. The genus *Bayardella* Burch includes two species, *B. johnei* and *B. cosmeta*, the latter once considered to be a species of *Glyptophysa*; 6. *Amerianna* Strand includes species with either a terminal or lateral pore on a simple pendant penis; 7. A new genus *Leichhardtia* is erected for the northern species *Bullinus sisurnius* Hedley 1918.

All these genera are placed in the planorbid subfamily Bulninae.

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The African planorbid *Bulinus* Müller, 1781 has become one of the best known and most intensely studied of all molluscs because of its role in the transmission of the human trematode parasite *Schistosoma haematobium* (Bilharz, 1852). Several Australian freshwater molluscs are morphologically similar to *Bulinus* and, as a consequence, this generic name has frequently been applied to lymnaeans from this country. This has not only caused confusion for taxonomists but has also supported the belief that snails capable of transmitting human schistosomes are present in Australia (Anon, 1972). The name *Bulinus* was first used by Adanson in 1757 in a description of a small freshwater mollusc from Senegal. Since the original description was pre-Linnean, Adanson cannot be quoted as author and Müller, who used the name in 1781, is now given authorship. In 1815, in a compilation of Müller's work, Oken emended the spelling to *Bullinus* and this form was subsequently widely adopted by authors until Pilsbry & Bequaert (1927) pointed out that

Bullinus Oken is an unnecessary emendation for *Bulinus* Müller, and has no status in nomenclature.

The classification of Australian bulniform planorbids has been confounded since its beginnings by a surfeit of species names and an ignorance of generic relationships. These problems have their origins in the traditional reliance of taxonomists on the molluscan shell as a major taxonomic character, an unfortunate choice in the light of the extreme variability of the freshwater Basommatophora. From 1826, with the description of *Physa novaehollandiae* by Blainville, until 1881 (Tate & Brazier, 1881), 54 species of *Physa* Draparnaud were named from Australia. Tate (1882) was convinced, however, that the sinistrally coiled Australian freshwater snails were not physids and stated "... in no instance have I found those distinctions which characterise *Physa* as separable from *Bulinus*. The mantle margin is neither expanded nor digitate".

Cooke (1889) also considered that the "So Called Physae of Australia" were related to *Bulinus*. He also

noted a similarity between some Australian species and the New Guinean *Physastra vestita* Tapparone-Canefri, 1883. This particular group differed from snails similar to *Physa newcombi* Adams & Angas 1863, and for these latter species Tate (1896) erected the genus *Isidorella*.

Iredale (1943) reviewed the classification of all known Australian freshwater gastropods. In dealing with the sinistrally coiled planorbids he examined 106 previously applied names and produced a checklist which included 59 species in six genera, all of which he placed in the family Bullinidae. In the following year Iredale (1944) described another genus, *Mutalena*, bringing the number of genera of Australian buliniform planorbids to seven. These seven genera, including 61 species, were: *Isidorella* Tate, 1896 (11 species), *Amerianna* Strand, 1928 (6 species), *Oppletora* Iredale, 1943 (1 species), *Glyptamoda* Iredale, 1943 (3 species), *Lenameria* Iredale, 1943 (37 species), *Tasmadora* Iredale, 1943 (1 species), and *Mutalena* Iredale, 1944 (2 species).

Hedley & Musson (1891) had commented "Upon few genera has synonymy, that curse of Babel upon Science, fallen heavier than upon the Australian *Bulinus*". In an attempt to solve this problem Hubendick (1948a) collated the scattered descriptions of the numerous molluscs included in *Bulinus* by various authors over about fifty years. Where possible, his investigation included detailed anatomical studies of representatives of the different groups of *Bulinus* s.l. He concluded that the most important character for distinguishing taxa, at least at the generic level, was the structure of the copulatory organ. Two very different forms were described, the normal pendant penis found in most Basommatophora, with the vas deferens opening either terminally or laterally, and the quite different pseudopenis or ultrapenis, which was restricted to two genera, *Bulinus* and *Indoplanorbis* Annandale & Prasad, 1920. Because of the unique nature of their copulatory organs, Hubendick segregated these genera into a subfamily, the Bulininae. He claimed, however, that studies on species previously included in Tate's genus *Isidorella* showed that these also had an ultrapenis and so must be synonymised with *Bulinus*. *Oppletora jukesii* was also synonymised with *Bulinus*. The other genera from Iredale's Bullinidae were included in the Planorbinae: *Lenameria* and *Tasmadora* were synonymised with *Physastra* and it was tentatively suggested that *Glyptophysa* Crosse and *Glyptamoda* Iredale could be synonyms of *Amerianna*. Hubendick's studies on *Bulinus* were extended to include all planorbids in his monograph 'Phylogeny in the Planorbidae' (Hubendick, 1955a) in which *Isidorella* and *Oppletora* were still included in the Bulininae as synonyms of *Bulinus*. These studies reduced Iredale's six genera to three - two synonymised with *Bulinus*, two with *Physastra* and one with *Amerianna*.

In a later article relevant to this discussion Hubendick (1964) demonstrated that the limpet-like

Ancylastrum Bourguignat from Tasmania, formerly placed in the Ancyliidae or Ferrissiidae, is actually a planorbid closely related to *Physastra*.

Hubendick's studies on planorbids were summarised by Zilch (1959) in his 'Handbuch der Palaozoologie', and this work formed the basis of the most recent discussion and summary of the taxonomic status of Australian freshwater molluscs by McMichael (1967). This author, however, includes *Isidorella* (with *Oppletora* as a synonym) as a valid genus in the subfamily Bulininae.

An important addition to the names applied to Australian planorbids is *Plesiophysa* (*Bayardella*) *johni* Burch, 1977. This small, neritiform species from Western Australia was placed in the neotropical genus *Plesiophysa* Fischer because both were thought to have a five-cusped rachidian tooth on the radula, a feature unique among planorbids.

In any discussion of the freshwater molluscs of Australia it is important to recognise that *Physa* now has a wide distribution on this continent, having been introduced from the northern hemisphere by human activity. It is found in all states, sometimes in isolated situations, but usually in and around large population centres. The species of *Physa* found in Australia is, at present, unknown despite the claim by Hubendick (1955b) that specimens of *Physa* in a collection of freshwater snails from Perth were *P. concinna* A. Adams & Angas, 1864, and that this was a truly indigenous representative of the genus. *P. concinna* was described from Arnhem Land and was, from the original description, clearly a species of *Physastra*.

With respect to the Australian buliniform planorbids Iredale's (1943) checklist was the culmination of classifications based primarily on shell characters. By studying internal anatomy Hubendick (1948a, 1955a) provided a broader foundation for a classification but the applicability of his work to the classification of Australian freshwater molluscs is limited because of doubts concerning the origins of the material on which his findings were based. The specimens of *Isidorella subinflata* (Sowerby) which he examined were collected in the Botanic Gardens in Lorenzo Marques, Mozambique by F. Linder in 1936 (Hubendick, 1948a). It was claimed that the species had been introduced from Australia and had been locally identified. The specimens of "*Bulinus dispar*" (Sowerby), which Hubendick examined and concluded should be referred to *Physastra*, were also collected in South Africa (in a private aquarium in Durban), and those he referred to *Physa gibbosa* (Gould), an Australian species with the type locality in Parramatta, Sydney, actually came from Mowewe, Southeast Celebes. Thus the only material definitely from Australia examined by Hubendick in his 'Studies on *Bulinus*' was a single unnamed species, from Tailem Bend in South Australia, which he placed in *Physastra*. Hubendick (1955a) presented details of the anatomy of one other species,

Amerianna obesa (H. Adams), from Queensland.

The positions taken by both Zilch (1959) and McMichael (1967) were based on acceptance of the anatomical work of Hubendick, without additional supporting evidence.

The proposition that *Glyptamoda* should be considered a synonym of *Glyptophysa* (Hubendick, 1948a; McMichael, 1967; Smith & Burn, 1976), while possibly correct, is also based entirely on similarity of shell structure, not on any knowledge of internal anatomy.

Materials and Methods

Sites of Collection of Mollusc Colonies. Sites of mollusc collections are listed in the appendix at the end of the paper.

Collection and Maintenance of Snail Colonies. Snails were collected from all suitable water bodies and air-freighted to Sydney. They were maintained in either glass aquaria or plastic food containers, in each case with a substratum of marble chips and in artificial pondwater made from distilled water with salts added (Ulmer, 1970). Snails were fed on autoclaved leaves and with a supplement made from dried lettuce, wheat germ and lucerne, ground in a blender. All aquaria were aerated. The colonies were kept in a room maintained at 25°C +/- 3°C. Lights were automatically switched on at 0600 hr and off at 1800 hr.

Examination Techniques. Apart from those sent to Sydney to start laboratory colonies, snails were preserved in the field for later studies. They were first relaxed with menthol crystals, usually overnight, then fixed in one of two ways. Specimens to be sectioned were fixed in aqueous Bouin's fluid, in which they remained for the duration of the field trip, and were then transferred to 70% ethanol with 5% glycerol added. Snails intended for museum collections were fixed in 10% formalin and stored in this solution. Comparison of a number of fixatives for the laboratory reared snails showed the superiority of Heidenhain's Susa and this was used for all laboratory reared specimens prior to sectioning. After fixation the schedule followed included alcohol dehydration, clearing in methyl benzoate and benzene and embedding in low melting point wax. Serial sections were cut at 5 micrometres and stained with Heidenhain's Azan. If possible, fresh specimens from laboratory colonies, as well as fixed material, were examined. In these cases the whole reproductive tract was removed, fixed in Baker's Formaldehyde Calcium and mounted in a lactophenol-PVA mixture to which Chlorazol Black had been added. This medium produced a permanent whole mount in which the tissues were cleared by the lactophenol and the nuclei stained by the Chlorazol Black.

Radulae were obtained by digesting the buccal mass of snails in a saturated solution of sodium hydroxide, washing in water and mounting in the

same lactophenol-PVA mountant used for whole mounts.

Drawings of radulae, whole mounts of copulatory organs and of serial sections were made with the aid of a drawing tube.

In the following discussion *Isidorella* is presented first because its anatomy is used to provide a basis for comparison with other taxa. The remaining genera are presented in chronological order of their original description.

The material examined in this study, dried shells, spirit preserved snails, serial sections and whole mounts of radulae and reproductive systems, is deposited in the Australian Museum, Sydney.

Specific Designations. No attempt has been made here to delineate species of *Isidorella*, *Glyptophysa* or *Amerianna* because the phenotypic plasticity of these snails makes such a task almost impossible if morphological criteria alone are used. It will be necessary for techniques such as isoenzyme electrophoresis to be applied if the validity of the 59 species listed by Iredale (1943) is to be assessed.

TAXONOMY

Class GASTROPODA

Order BASOMMATOPHORA

Family Planorbidae Rafinesque, 1815

Diagnosis. Small to medium sized snails; anatomically sinistral; with long slender tentacles; accessory respiratory structure, the pseudobranch, developed as an outgrowth of the left body wall; blood containing haemoglobin. Shell and internal anatomy, especially the copulatory organ, extremely variable; simultaneous hermaphrodites; egg capsule three layered.

Subfamily Bulininae

Diagnosis. Subfamily as defined by Hubendick (1978). Shell morphology variable; pseudobranch usually secondarily folded. Prostate diverticula arise from one small area of the sperm duct. Gonad acini arranged in a fan-like pattern.

Genus *Isidorella* Tate, 1896

Figs 1-4

Isidorella Tate, 1896: 212. Type species *Physa newcombi* A. Adams & Angas, 1863. Recent, Australia.

Diagnosis. Bulinine snails with a subglobose to oval shell having unshouldered whorls; copulatory organ lacking accessory bursa or flagellum, pendant penis is biramous, prostatic duct absent.

Description. SHELL. (Fig. 2a) Sinistraly coiled, umbilicate, subglobose to oval; whorls rounded with indented sutures. Aperture large, ovate; parietal lip evenly curved without columella fold or plait. Transverse growth lines common forming prominent ridges on surface of some shells. Spiral

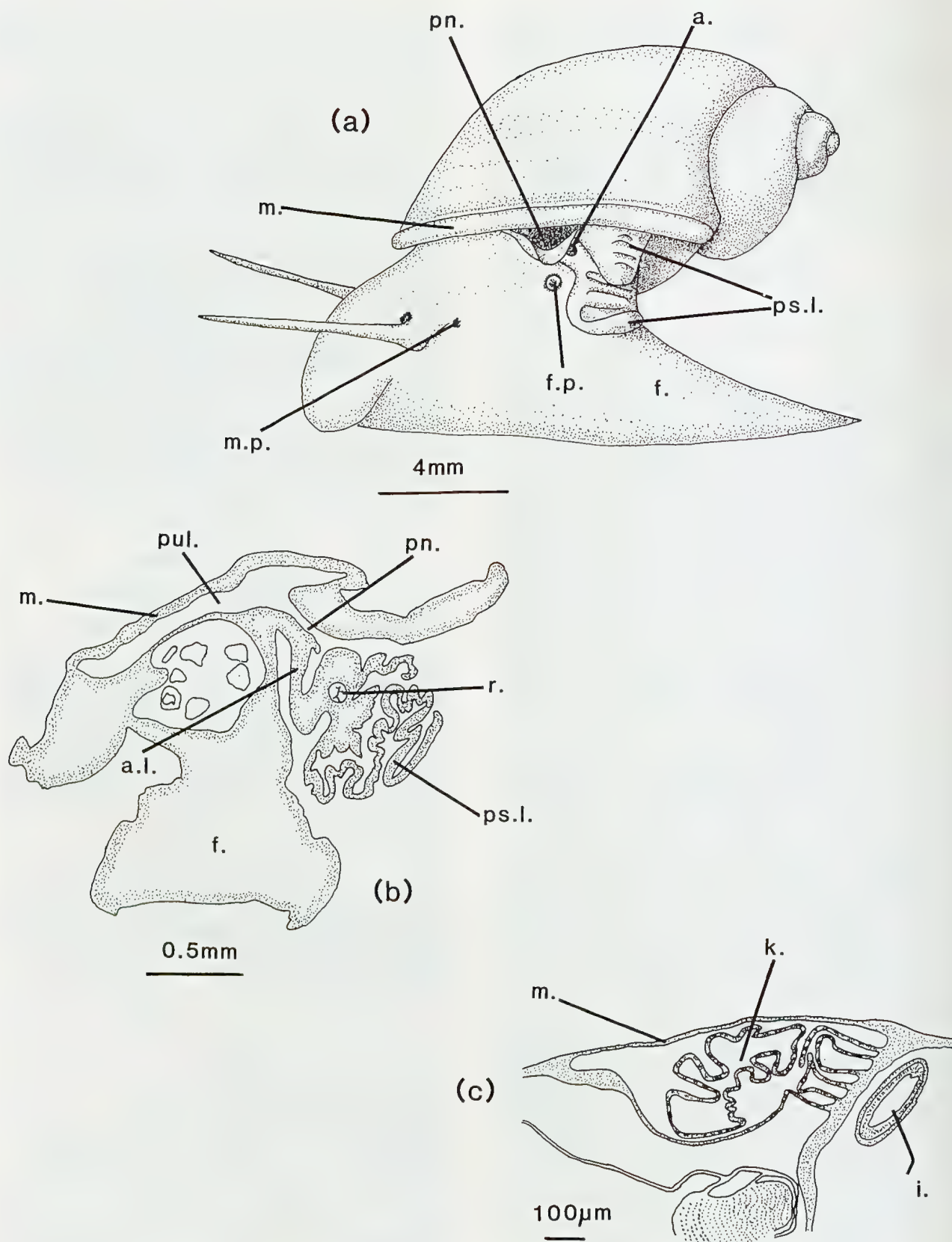


Fig.1. (a) *Isidorella newcombi* - left side; (b) *I. newcombi*, t.s. showing pseudobranch; (c) l.s. of mantle showing kidney. a. anus; a.l. anal lobe; f. foot; f.p. female genital pore; i. intestine; k. kidney; m. mantle; m.p. male genital pore; pn. pneumostome; ps.l. pseudobranch lobes; pul. pulmonary cavity; r. rectum.

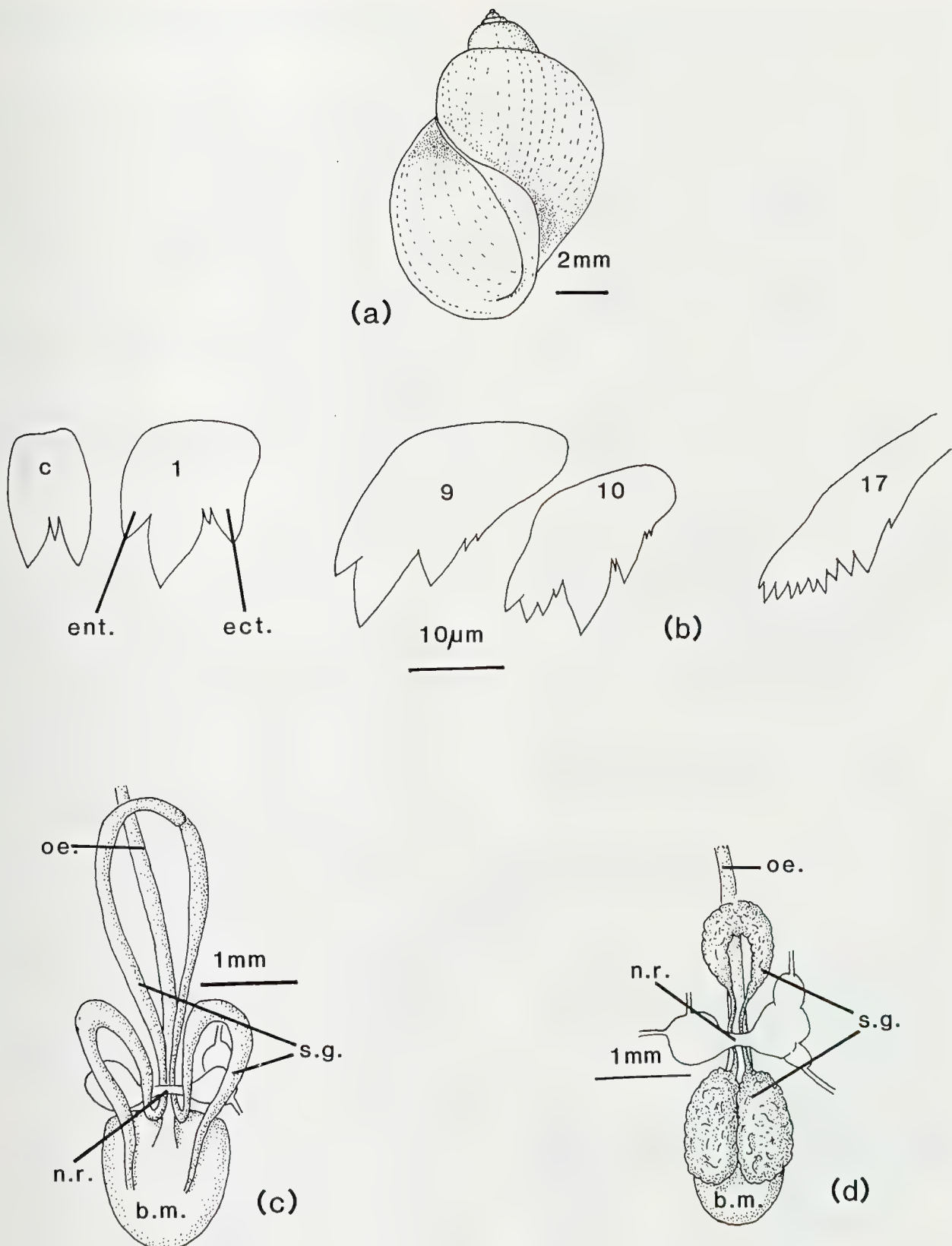


Fig.2. (a) shell of *Isidorella newcombi*; (b) radula of *I. newcombi*: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; (c) salivary glands of *Bulinus africanus*; (d) salivary glands of *I. newcombi*. b.m. buccal mass; ect. ectocone; ent. entocone; oe. oesophagus; n.r. nerve ring; s.g. salivary glands.

rows of periostracal hairs frequently present, especially on shells of young snails.

EXTERNAL MORPHOLOGY. Body pigmentation red; foot elongate, pointed posteriorly; tentacles long, circular in cross section, arising from broad, flat base on sides of head. Eyes situated medially, at base of tentacles. Male genital pore immediately posterior to left tentacle; female genital pore opening through small, slightly elevated papilla, above and posterior to male opening. Pneumostome, pseudobranch and anal lobe situated on left side in vicinity of posterior of shell aperture (Fig. 1a). Rectum opening at tip of anal lobe which bears pseudobranch folds, shorter outer lobe overlapping top of inner lobe; pseudobranch lobes secondarily folded. Anal lobe, an outgrowth of body wall, suspended in mantle cavity (Fig. 1b).

RADULA (Fig. 2b). Central tooth has 2 equal sized cusps, separated by small denticle in radulae from most populations. Lateral teeth tricusped, usually with denticles between mesocone and ectocone. Some lateral teeth bear small denticle on lateral edge of ectocone. Cones of lateral teeth triangular, sides usually slightly convexly curved. Transition from lateral to marginal teeth beginning in vicinity of lateral teeth 6–10, marked by a splitting of ectocone into numerous smaller cusps. Marginal teeth exhibit great reduction in size of ectocone and splitting of ectocone into many smaller cusps. Mesocone gradually reduced in size and by tooth 20 only slightly larger than entocone cusps.

SALIVARY GLANDS. (Fig. 2d). Salivary glands form 2 broad sheets of tissue lying on top of buccal mass; narrow to thin tubes where they pass through nerve ring; join posteriorly, over oesophagus; ducts enter anterior of buccal mass.

MANTLE AND ASSOCIATED STRUCTURES. Kidney traverses inside of mantle, from right to left; distal end reflexed. Renal ridges or folds absent (Fig. 1c); rectal ridge absent.

REPRODUCTIVE SYSTEM. Copulatory organ. Copulatory organ without accessory glands or flagella. Penis sheath $\frac{1}{4}$ length of praeputium, (Fig. 3b). Biramous, pendant penis (Fig. 3c). Lumen of vas deferens at proximal end of penis wide and strongly ciliated; opening of vas deferens between 2 rami of penis.

Prostate gland. Acini radiate from one point; no collecting prostatic duct present (Fig. 4a).

Insertion of bursa copulatrix. Duct of bursa inserts at distal end of vagina, just inside the body wall (Fig. 4c).

Distribution. Australian mainland with the exception of the Kimberley region, Arnhem Land and northern Queensland. The genus may be absent from Tasmania. I have examined many specimens in museum collections labelled *Isidorella* with reliable information fixing the collection site in Tasmania. All have proved to be specimens of *Glyptophysa*.

Comments. From the information presented above it can be concluded that *Isidorella* is not closely related to *Bulinus*. Several substantial differences are noted.

In discussing the supposed similarity between *Bulinus* and *Isidorella*, Hubendick (1948b) described the salivary glands as being tubular and joining behind the circumoesophageal nerve ring in both taxa. Studies of laboratory colonies of *B. truncatus*, *B. tropicus* and *B. liratus* held at the School of Public Health and Tropical Medicine, University of Sydney, and of preserved material of *B. africanus*, have all confirmed Hubendick's description for *Bulinus* (Fig. 2c). In no instance, however, has a specimen of *Isidorella* from any locality in Australia shown similar morphology of the salivary glands. They are invariably in the form of flat sheets, as described above.

In *Bulinus* the duct of the bursa copulatrix inserts at the proximal end of the vagina (Fig. 4b) but that of *Isidorella* inserts at the distal end, just inside the body wall (Fig. 4c).

The major difference between *Bulinus* and *Isidorella* is in the nature of the copulatory organ, the feature Hubendick (1948a) described as their major similarity, and the basis for his synonymising of the two genera. When the copulatory organs are examined superficially some similarity is apparent; in both cases they are relatively simple structures without accessory glands or flagella, with a clear demarcation between the praeputium and the penis sheath. Closer examination reveals that the relative dimensions of these two parts of the organ differ. The penis sheath of *Isidorella* is relatively short; only one quarter of the length of the praeputium. The two sections are approximately equal in length in most *Bulinus* (Fig. 3a,b). The internal anatomy of the two organs differs significantly. *Isidorella* has a pendant penis, while *Bulinus* has the characteristic pseudopenis or ultrapenis (Hubendick, 1948, 1955a). The ultrapenis (Fig. 3d) consists of a long, coiled, eversible tube which is attached at both the upper and lower end of the penis sheath. This tube is separated from the wall of the penis sheath by an extensive sinus which appears to have arisen as a result of splitting of the musculature. This is indicated by the lack of any epithelium on the inside of the sheath or on the periphery of the coiled tube (Fig. 3e).

The penis of *Isidorella* shows considerable variation, apparently related to individual reproductive status. In some specimens collected at random and in animals killed at the time of copulation, transverse sections show extensive development of the ciliated epithelium on the outside of the penis and an increase in the size of the two projections below the opening of the vas deferens (Fig. 3f). In other specimens from the same populations the ciliated epithelium is less prominent and the digitations smaller.

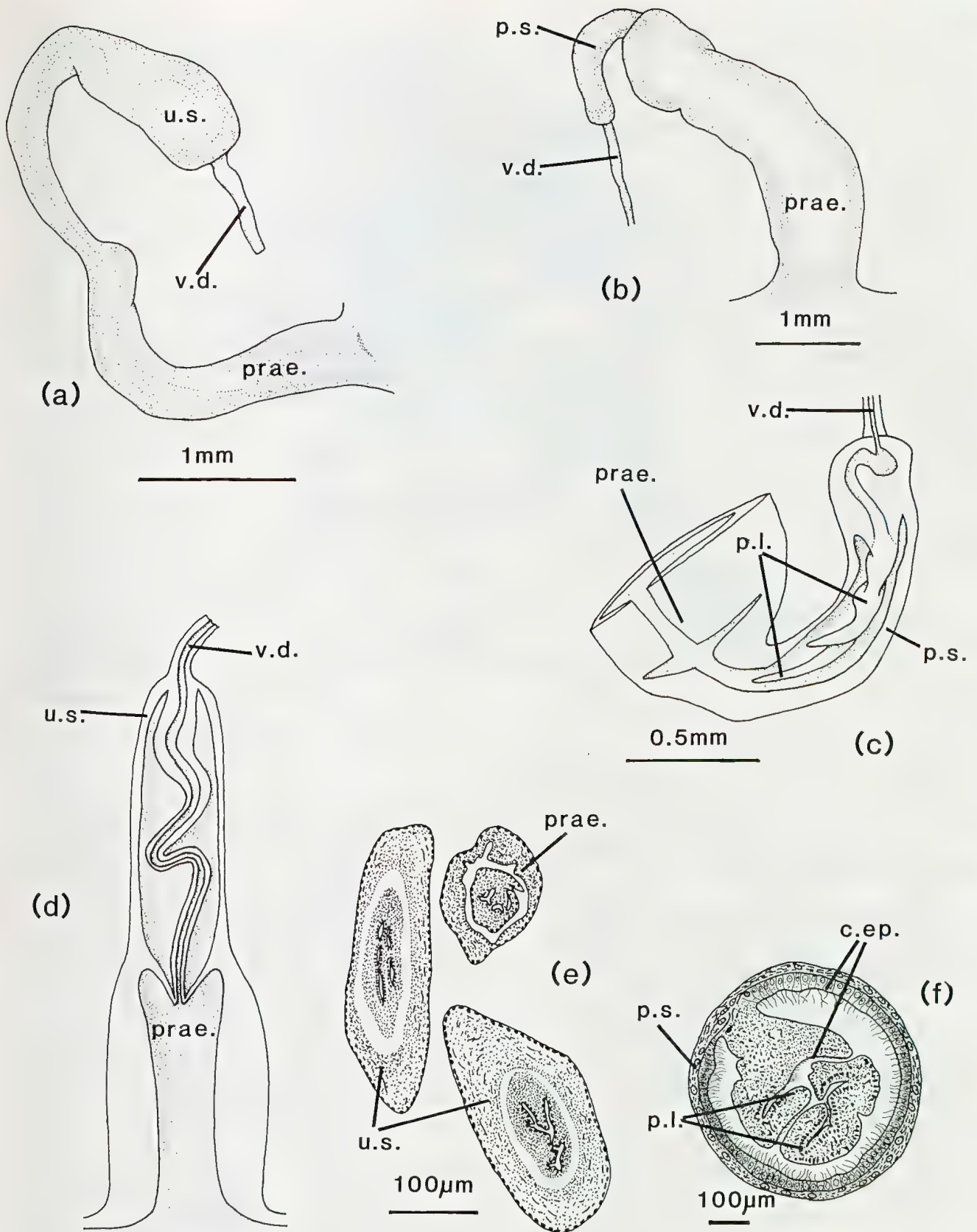


Fig.3. (a) copulatory organ of *Bulinus africanus*, external view; (b) copulatory organ of *Isidorella newcombi*, external view; (c) diagrammatic section of penis of *Isidorella*; (d) diagrammatic section of ultrapenis of *Bulinus*; (e) t.s. of ultrapenis of *B. africanus*; (f) t.s. penis sheath of *Isidorella*. c.ep. ciliated epithelium; p.l. lobes of penis; prae. praeputium; p.s. penis sheath; u.s. ultrapenis sheath; v.d. vas deferens.

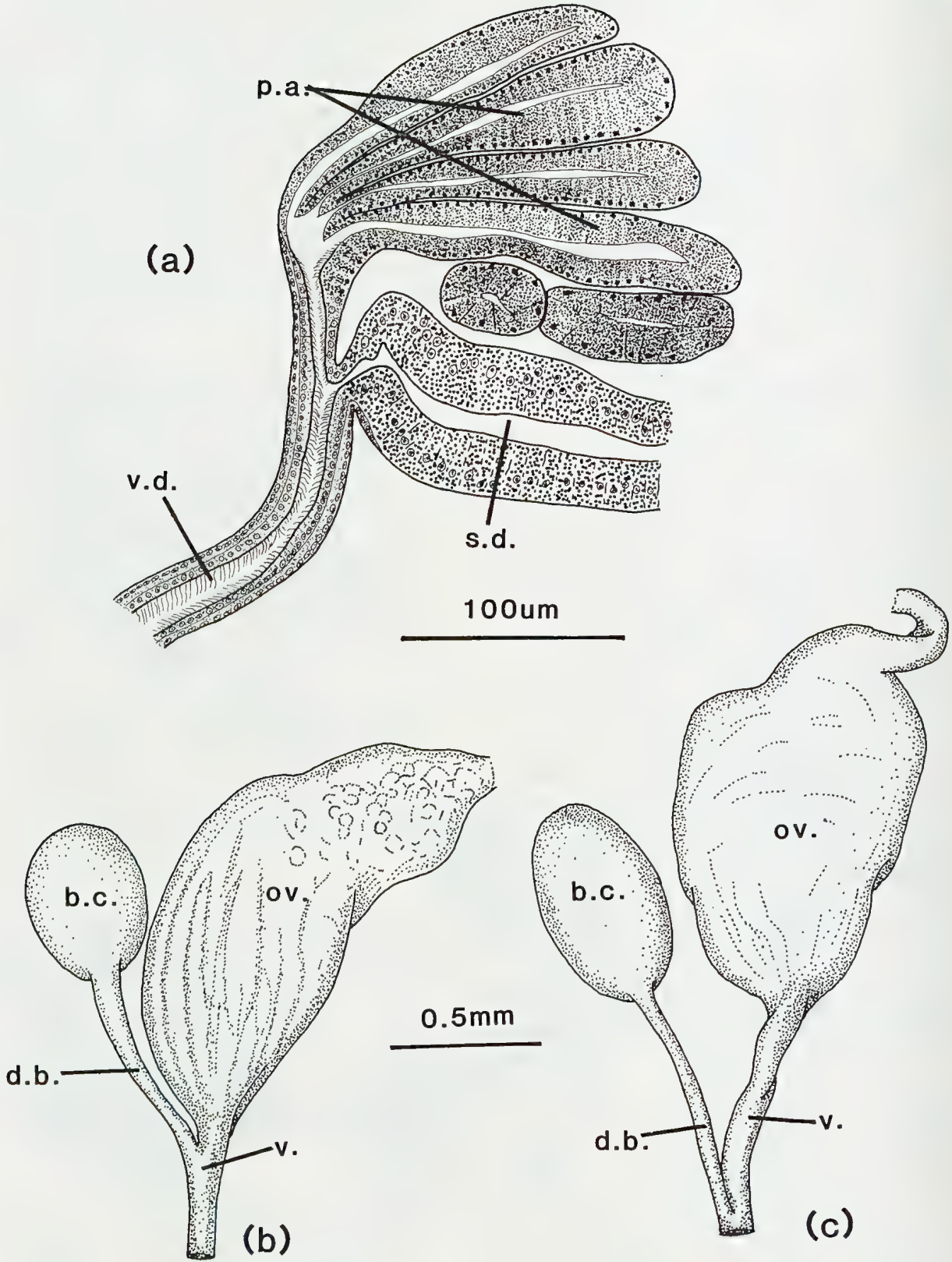


Fig.4. (a) section through part of prostate gland of *Isidorella newcombi*; (b) distal end of female reproductive tract of *Bulinus*; (c) distal end of reproductive tract of *Isidorella*. b.c. bursa copulatrix; d.b. duct of bursa copulatrix; ov. oviduct; p.a. prostate acini; s.d. sperm duct; v. vagina; v.d. vas deferens.

These are the major obvious differences between *Bulinus* and *Isidorella*; in many other respects the two taxa are similar. There are obvious similarities in the general shell morphology, though there is a greater range of shape in *Bulinus*. The broad details of the radulae of these two genera are similar. The anatomy of the alimentary tract of *Isidorella* has not been studied in sufficient detail yet for strict comparison with that of *Bulinus*. Despite Wright's (1961) claim to the contrary, there is no significant difference between the prostate glands of these two genera.

The experience gained in this study indicates that there are no clearcut characters distinguishing between various geographically distinct isolates of *Isidorella*. This was also the conclusion reached by Tate (1896). As a consequence all specimens examined here have been referred to the type species, *I. newcombi*. The localities from which *Isidorella* was collected are listed in the appendix.

Details of the anatomy of the other Australian buliniform planorbids presented subsequently indicate that *Isidorella* is generically distinct.

Hubendick (1958) described the anatomy of *Protancylus adhaerens* P. & F. Sarasin from Sulawesi. This species has a penis with two elongate processes below the lateral opening of the vas deferens. The rest of the anatomy differs markedly from that of *Isidorella* so, unless further study indicates otherwise, the similarity of penis structure should be regarded as a result of convergence.

Ancylastrum Bourguignat, 1883

Figs 5, 6

Ancylastrum Bourguignat, 1853: 63. Type species *Ancylus* (*Ancylastrum*) *cumingianus* Bourguignat, 1853; subsequent designation Bourguignat 1853: 170. Recent, Tasmania.*

Legrandia Legrand, 1879: 95. Type species *Ancylus cumingianus* Bourguignat, 1853. *Cumingia* Clessin, 1880: 14. Type species *Ancylus cumingianus* Bourguignat, 1853. Not *Cumingia* Sowerby, 1833.

Tasmancylus Iredale, 1926: 115. Type species *Ancylus cumingianus* Bourguignat, 1853.

Diagnosis. Patelliform bulinine snails; mesocone of lateral teeth rounded with small denticles; copulatory organ having a flagellum, lacking an accessory bursa, penis biramous with a terminal stylet on one ramus or uniramous with a subterminal augur-like fold; bursa copulatrix spatulate; rectal ridge absent.

Description. **SHELL.** Shell limpet-like, asymmetrical (Fig. 5a). Heterostrophic; apical portion a vestigial spire, projects to right, consists of almost a complete whorl. Apical region with poorly

developed spiral striations. Abrupt change between apex and main body of shell which is patelliform; most specimens of *A. cumingianus* have a smooth surface broken by concentric growth lines; some specimens of this species have faint radiating ribs; ribs strongly developed on shell of *A. irvinae*.

EXTERNAL MORPHOLOGY. Body limpet-like; edge of mantle surrounding foot (Fig. 5b); tentacles very short, (this may be a result of the state of fixation of the available material); eyes situated on anteroventral side of tentacle base; pseudobranch unilobed without strong folding (Fig. 5c); rectum opens on anterior margin of pseudobranch, directed posteriorly. Opening of pulmonary cavity a small slit, high on side of body, anterior to pseudobranch.

RADULA (Fig. 5d,e). Central tooth bicusped, cusps with straight inner and curved outer margins (*A. cumingianus*), or equally curved on each side (*A. irvinae*). Lateral teeth with broad, serrated mesocones and small entocones and ectocones. Gradual transition to marginal teeth (*A. irvinae*); by tooth 10 mesocone has narrowed and ectocone is much longer. Marginal teeth with 3 prominent cusps separated by small denticles; denticles also present on lateral edges of entocone and ectocone. No marked development of marginal teeth in *A. cumingianus*.

SALIVARY GLANDS. Salivary glands flat sheets with ribbon-like posterior portions passing through circumoesophageal nerve ring.

REPRODUCTIVE SYSTEM. Copulatory organ. Muscular flagellum, joining penis sheath at same point as insertion of vas deferens. Penis of *A. irvinae* bilobed (Fig. 6a,b). One lobe bears a terminal stylet; second bears, terminally, opening of vas deferens. Penis of *A. cumingianus* unilobed with terminal stylet. Proximal to stylet is an augur-like fold of penis epithelium. Opening of vas deferens occurs in this region (Fig. 6d). Nature of prostate gland not determined.

Bursa copulatrix. Bursa copulatrix spatulate (Fig. 6c), duct inserts into distal end of vagina.

Gonad. Gonad proportionally larger than that of other Australian planorbids; completely separated from folds of digestive gland.

Distribution. Highland lakes in Tasmania.

Comments. *Ancylastrum* is related to *Glyptophysa* but is sufficiently different to warrant separate generic placement. This study confirms Hubendick's (1964) findings on the genus and also confirms the validity of the two species described. This conclusion is contrary to that of Johnston (1888), who rejected *A. irvinae* Petterd because he considered the differences in the shells represented the extremes of a continuum.

Glyptophysa Crosse, 1872

Figs 7, 8

Glyptophysa Crosse, 1872: 151. Type species *Physa petiti* Crosse 1872; monotypy. Recent, New Caledonia.

*The validity of the name *Ancylastrum* was discussed by Hubendick (1952), and was confirmed by the International Commission of Zoological Nomenclature in its Opinion 364. Bourguignat did not designate the type species in the original description in February 1853, but did so in May of that year.

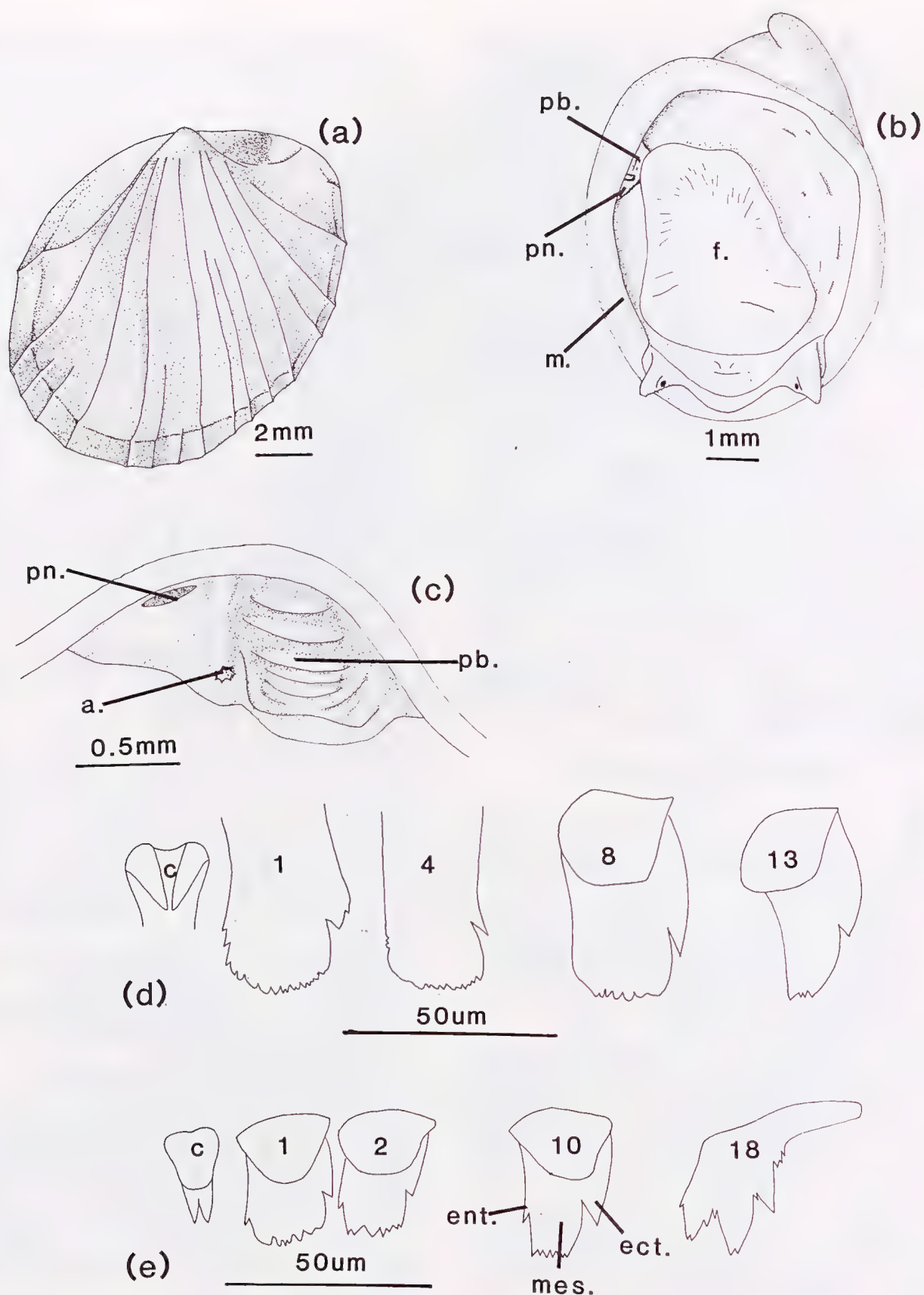


Fig.5. Anatomy of *Ancylastrum*. (a) shell of *A. irvinae*; (b) *A. irvinae*, ventral view; (c) *A. irvinae*, pseudobranch; (d) radula, *A. cumingianus*: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; (e) radula *A. irvinae*. a. anus; ect. ectocone; ent. entocone; f. foot; m. mantle; mes. mesocone; pb. pseudobranch; pn. pneumostome.

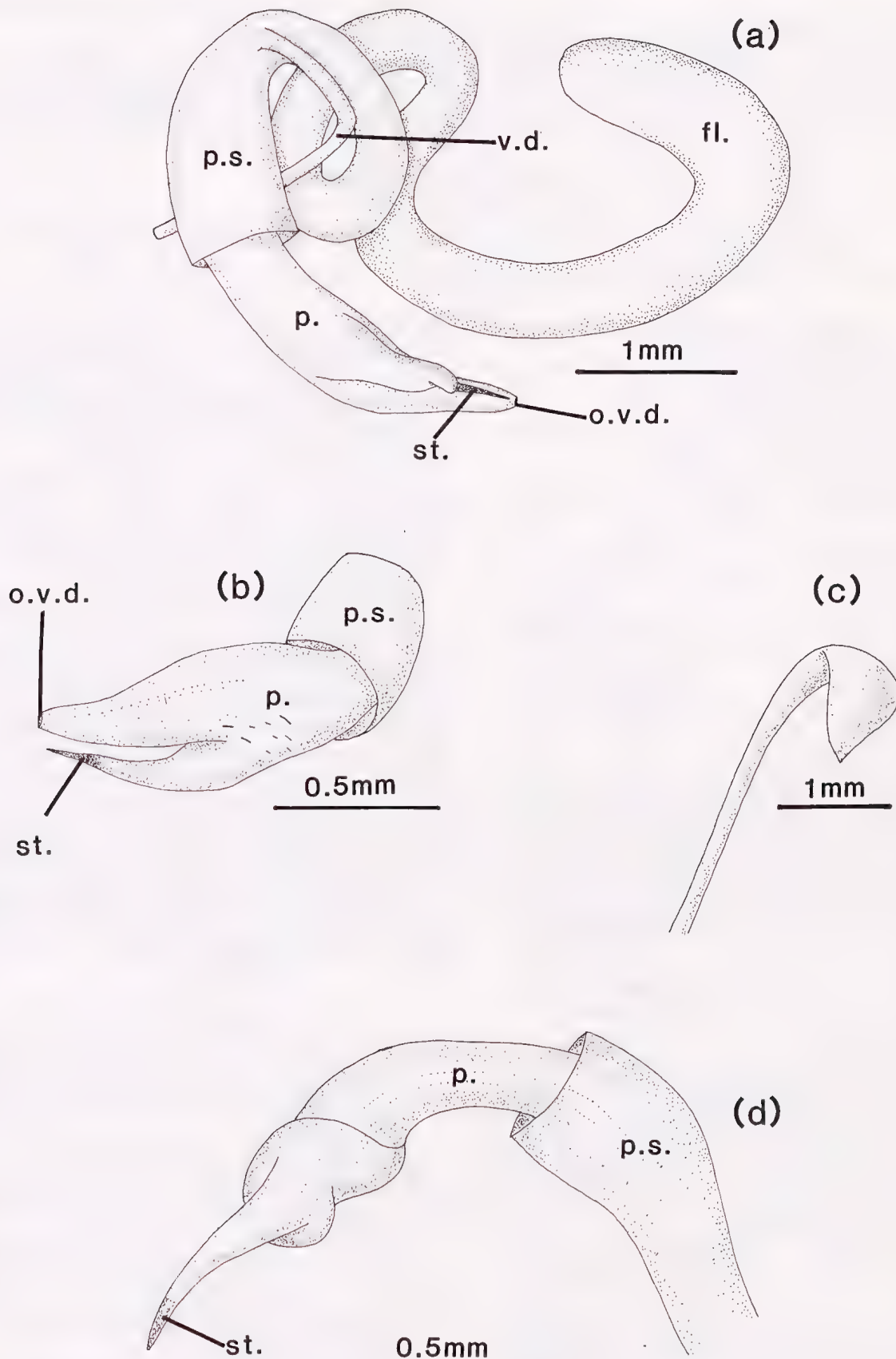


Fig.6. *Ancylastrum*, continued. (a) *A. irvinae*, copulatory organ - penis exposed; (b) bifid penis of *A. irvinae*; (c) *A. cumingianus*, bursa copulatrix. (d) *A. cumingianus*, penis; fl. flagellum; o.v.d. opening of vas deferens; p. penis; p.s. penis sheath; st. stylet; v.d. vas deferens.

Diagnosis. Bulinine snails with the shell varying from globose to high spired, with smooth surface or spiral lirae, whorls round or carinate, distinct columellar fold present; copulatory organ with a flagellum, lacking an accessory bursa, penis uniramous with terminal stylet, bursa copulatrix

globose; rectal ridge present; single renal ridge on roof of pulmonary cavity.

Remarks. Two subgenera are recognised within *Glyptophysa*. The nominate subgenus is widespread and encompasses species previously included in *Physastra* Tapparone-Canefri, 1883.

Key to the Subgenera of *Glyptophysa* (based on shell characters)

1. Shell elongately conic to oval; whorls rounded or carinate; spire prominent. *Glyptophysa*
——Shell globose; whorls flattened; spire depressed. *Oppletora*

Subgenus *Glyptophysa* s.s.

In addition to *Glyptophysa* Crosse the following taxa are included in this subgenus.

Physastra Tapparone-Canefri, 1883: 246. Type species *Physa* (*Physastra*) *vestita* Tapparone-Canefri, 1883; monotypy. Recent, New Guinea.

Lenameria Iredale, 1943: 215. Type species *Physa gibbosa* Gould, 1847; original designation. Recent, Parramatta, N.S.W.

Glyptamoda Iredale, 1943: 220. Type species *Physa aliciae* Reeve, 1862; original designation. Recent, southeastern Australia.

Tasmadora Iredale, 1943: 221. Type species *Physa aperta* Sowerby, 1874; original designation. Recent, Hamilton, Tasmania.

Mutalena Iredale, 1944: 121. Type species *Mutalena reperta* Iredale, 1944; original designation. Recent, western New South Wales.

Description. SHELL. (Fig. 7 a,b). Sinistral; elongately conic to oval; whorls carinate, rounded with indented sutures or shouldered; body whorl smooth or with prominent lirae having a serrated appearance resulting from small projections of periostracum; aperture pyriform to oval, posterior of outer lip angulated or evenly curved, columella with a distinct fold; spire of from 2–6 whorls may be truncate.

EXTERNAL MORPHOLOGY. Externally similar to *Isidorella*, except that foot has a rounded posterior end in *Glyptophysa*.

RADULA (Fig. 7 d,e). Central tooth with 2 equal cusps separated by a denticle; tricusped lateral teeth have denticles between major cusps; transition to marginal teeth gradual, number of ectocone denticles and entocone cusps progressively increasing; mesocone and ectocone of marginal teeth progressively decrease in size with increasing distance from centre of radula.

SALIVARY GLANDS. Flat sheets of tissue, pass through nerve ring; ducts insert into top of buccal mass.

MANTLE AND ASSOCIATED STRUCTURES. Prominent ridge on inner surface of mantle; ridge on ventral surface of kidney; distal end of rectum bears a ridge which forms outer pseudobranch lobe.

REPRODUCTIVE SYSTEM. Copulatory organ. Muscular flagellum joins penis sheath at insertion of

vas deferens (Fig. 8a); penis with lateral pore and terminal stylet (Fig. 8b). The copulatory organ figured (Fig. 8c) was everted when snail was fixed and demonstrates form taken during copulation.

Prostate gland and bursa copulatrix. Both organs similar to those described for *Isidorella*.

Distribution. Australia, New Guinea, New Caledonia, New Zealand, Moluccas, Philippines, Sumatra, islands of South Pacific east to Tahiti, Malaysia (introduced). The number and distribution of species in this subgenus is uncertain.

Comments. Specimens of the type species from New Caledonia have not been examined in this study. However, Starmühlner (1970) has adequately described *G. petiti* and his description would be equally applicable to *Physa aliciae*, the type species of Iredale's genus *Glyptamoda*. Whether this species should be synonymised with *G. petiti* can only be determined by further study. *G. aliciae* has been compared in detail with species previously included in *Physastra*, *Lenameria*, *Tasmadora* and *Mutalena*. The only differences noted relate to shell shape and sculpture. Meier-Brook (1983) and Brown (1980) have both described a range of variation within the planorbid genera *Gyraulus* and *Bulinus* respectively which exceeds that between these four Australasian taxa.

Subgenus *Oppletora* Iredale 1943

Oppletora Iredale & Whitley, 1938: 64. (Nomen nudum).
Oppletora Iredale, 1943: 222. Type species *Physopsis jukesii* H. Adams, 1861; original designation. Recent, northern Australia.

Description. SHELL. Shell sinistral, globose, spire markedly depressed, body whorl constitutes most of shell (Fig. 7c). Aperture oval, well-developed columellar fold.

EXTERNAL MORPHOLOGY. External anatomy similar to that of *Glyptophysa*. Foot rounded posteriorly; rectal lobe folded to form outer pseudobranch lobe (Fig. 8e). Pigmentation of foot and mantle relatively slight.

RADULA (Fig. 7f). Central tooth bicusped, lacks central denticle. First lateral teeth tricusped with a denticle between the mesocone and ectocone. Early transition to marginal teeth; ectocone of tooth 4

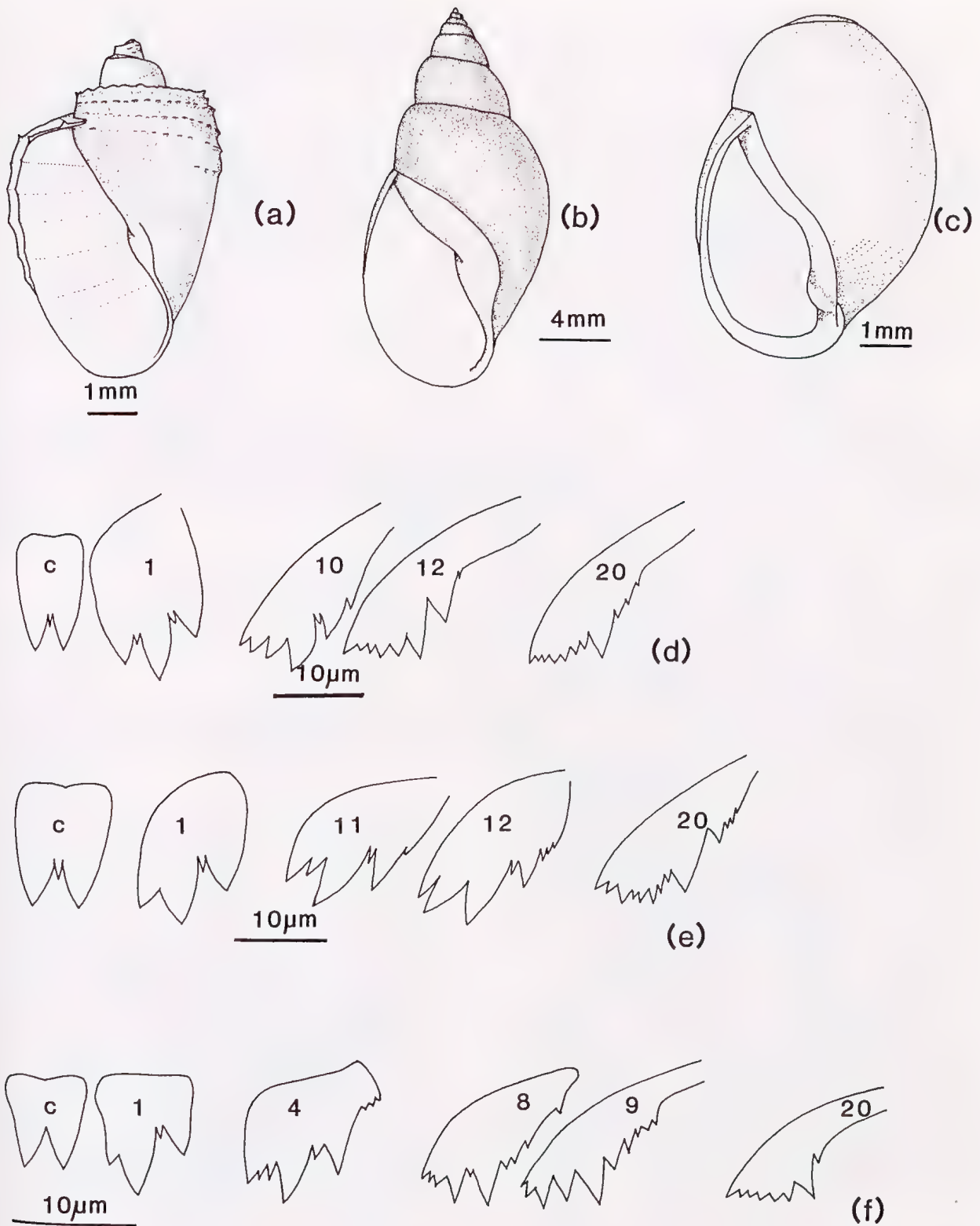


Fig.7. Anatomy of *Glyptophysa*. (a) shell of *G. aliciae*; (b) shell of *G. concinna*; (c) shell of *G. (Oppletora) jukesii*; (d) radula of *G. aliciae*; (e) radula of *G. concinna*; (f) radula of *G. (Oppletora) jukesii*.

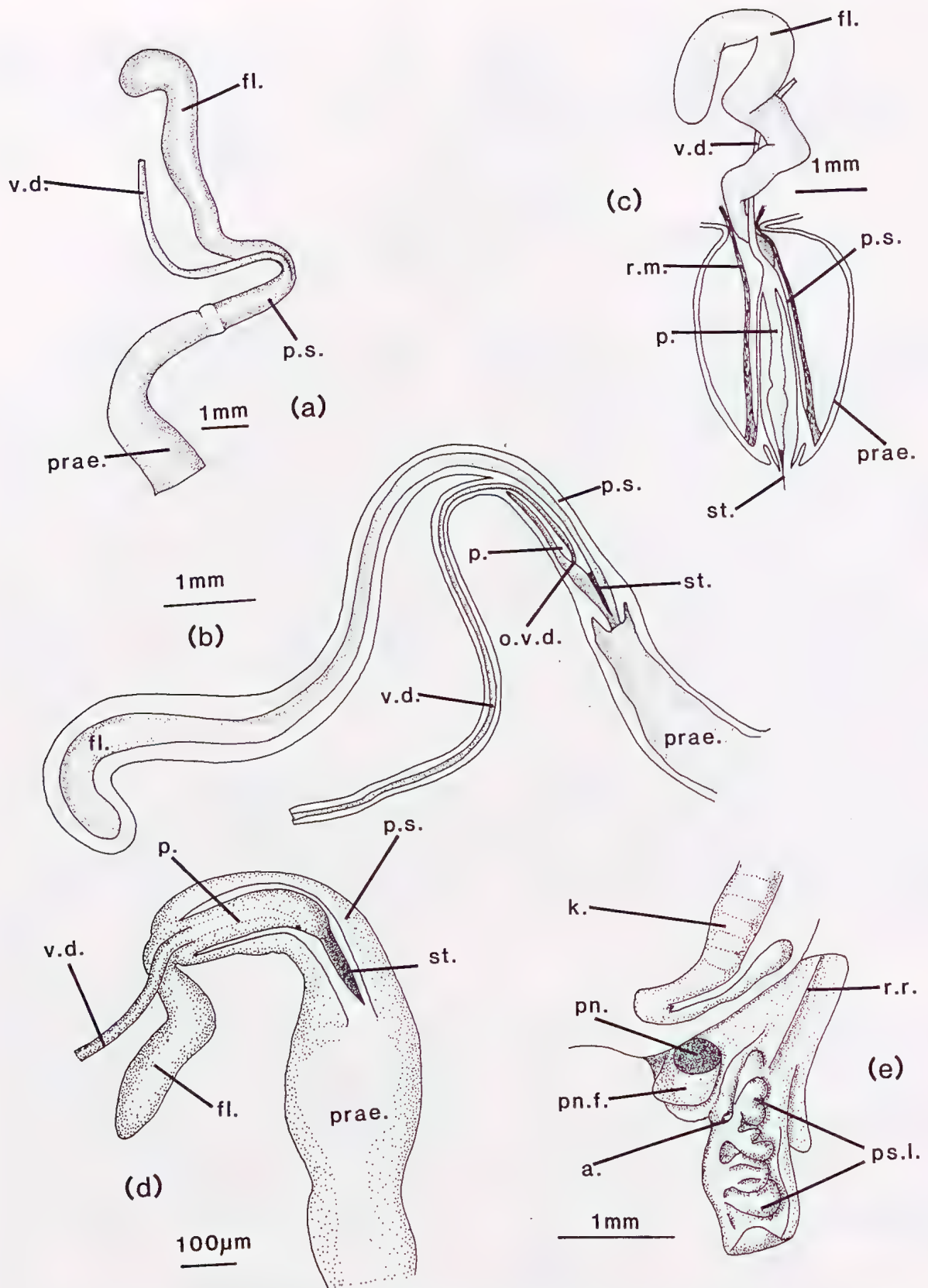


Fig.8. Anatomy of *Glyptophysa* continued. (a) copulatory organ of *G. concinna*, external view; (b) copulatory organ of *G. concinna*, internal structure; (c) copulatory organ of *G. aliciae*, internal structure, penis everted; (d) copulatory organ of *G. (Oppletora) jukesii*, external view; (e) pseudobranch of *G. (Oppletora) jukesii*. a. anus; fl. flagellum; k. kidney; o.v.d. opening of vas deferens; p. penis; pn. pneumostome; pn.f. pneumostome fold; prae. praeputium; p.s. penis sheath; ps.l. pseudobranch lobes; r.m. retractor muscles; r.r. rectal ridge; st. stylet; v.d. vas deferens.

divided into 3 small cusps, denticles at base of ectocone. Extreme marginal teeth comb-like with a much divided entocone and reduced ectocone.

SALIVARY GLANDS. The salivary glands are similar to those described for *Isidorella*.

REPRODUCTIVE SYSTEM. Copulatory organ. Copulatory organ with flagellum relatively shorter and stylet relatively longer than for *Glyptophysa* s.s. Opening of vas deferens lateral (Fig. 8d).

Prostate gland. No collecting ducts for the prostate acini.

Bursa copulatrix. Bursa copulatrix globose, duct inserts distally on vagina.

Distribution. There is a single species with a patchy distribution from the Kimberley region to Arnhem Land.

Comments. *Oppletora* is most closely related to *Glyptophysa*. Whilst the differences, mainly in shell shape and in the relative proportions of organs, are consistent, they are relatively minor by comparison with those between genera such as *Isidorella* and *Glyptophysa*. *Oppletora* is placed as a subgenus within *Glyptophysa*.

Genus *Amerianna* Strand, 1928

Figs 9, 10

Ameria H. Adams, 1861: 143. Type species *Physa* (*Ameria*) *carinata* H. Adams, 1861. Not *Ameria* Walker, 1854, Lepidoptera.

Amerianna Strand, 1928: 63. Type species *Physa* (*Ameria*) *carinata* H. Adams, 1861; original designation. Recent, Boyne River, Queensland. New name for *Ameria* H. Adams, 1861.

Diagnosis. Buline snails having a carinate shell with a truncate spire; copulatory organ a uniramous, pendant penis with a terminal or lateral pore; bursa copulatrix elongate; 3 ridges on roof of pulmonary cavity, rectal ridge present.

Description. **SHELL.** (Fig. 9a,b) Sinistral, cylindrical shell; spire normally truncate, rarely elevated. Body whorl strongly keeled or with rounded shoulders. Aperture almost as long as shell, angular posteriorly, narrowly curved anteriorly. Slight columellar fold. Surface usually smooth; some specimens, especially juveniles, with spiral rows of periostracal hairs.

EXTERNAL MORPHOLOGY. Heavy body pigmentation masks haemoglobin with speckled grey. Pseudobranch more extensively folded than in other genera described (Fig. 9d); fused to mantle edge at anterior, upper margin.

RADULA (Fig. 9c). Central tooth bicusped without denticle between cusps; cusps of equal size. Lateral teeth tricusped with denticle between the mesocone and ectocone. Transition to marginal teeth begins at about tooth 12 which has prominent ridges on the base lateral to ectocone. Tooth 13 similar but shows slight splitting of entocone; this change progresses laterally in combination with subdivision of ectocone.

SALIVARY GLANDS. Branched, flat plates; pass through circumoesophageal nerve ring. Ducts insert into top of buccal mass.

MANTLE AND ASSOCIATED STRUCTURES. Three small ridges traverse inside of mantle roof; one anterior, two posterior to kidney (Fig. 9e).

REPRODUCTIVE SYSTEM. Copulatory organ. Demarcation between penis sheath and praeputium not pronounced; accessory structures lacking; simple pendant penis. Opening of vas deferens terminal or lateral (Fig. 10a,b). Praeputium with irregular muscular folds on internal wall.

Prostate gland. Prostate gland with separate prostatic duct leading from base of acini to junction of sperm duct and vas deferens (Fig. 10c).

Bursa copulatrix. Bursa copulatrix elongate oval; duct inserts into distal end of vagina.

Distribution. Northern regions of Australian mainland, New Guinea, Moluccas, Philippines. Introduced into Java (Butot, 1954), Thailand (Brandt, 1974) and Nigeria (Brown, 1983). The number of species and their distribution is uncertain.

Comments. Throughout its range within the Australian/Southwest Pacific region *Amerianna* exhibits considerable variation in shell morphology, though the majority of described species have shortened spires and most are carinate. All have a simple pendant penis, but the opening of the vas deferens may be terminal or lateral. Because the two kinds of penis are found in snails with similar shell morphology, it is not yet possible to conclude with certainty the position of the type species *A. carinata*. Brown (1983) did, however, illustrate a penis with a terminal pore for specimens he concluded were *A. carinata* collected at Ibadan, Nigeria. These were compared with specimens from the type series held in the British Museum (Natural History). There is no clear pattern of geographic separation of the two forms.

Cotton (1943) erected the subgenus *Ameriella* for *A. bonushenricus* because of the distinctive shell morphology. Walker (1985) retained this division for species of *Amerianna* with a lateral penis pore, and included in the subgenus *Bullinus sisurnius* Hedley 1918. This species was included because of the form of its penis and its possession of a prostatic collecting duct. Further examination of material of this species has led to the conclusion that *B. sisurnius* is generically distinct. It is discussed later in this review.

Until further studies are performed on this genus as a whole, no decision on the number of subgeneric taxa can be made and there appears to be insufficient reason to use *Ameriella* as a subgenus. Two forms distinguishable on shell morphology, *A. carinata* and *A. bonushenricus* are present in Australia, but both kinds of penis structure are found in snails with carinata-like shells. The number of species of *Amerianna* from outside Australia is also uncertain,

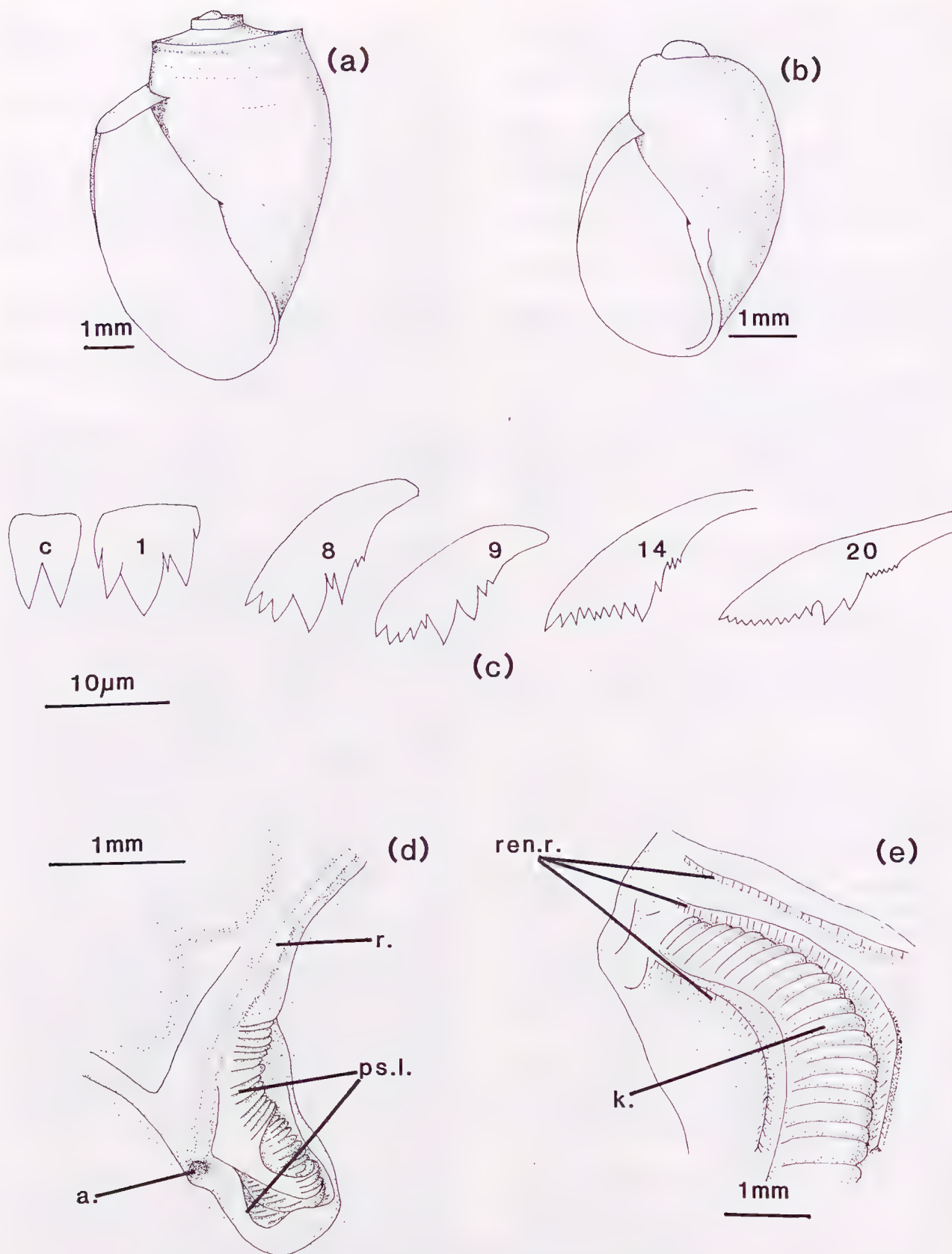


Fig.9. Anatomy of *Amerianna*. (a) *A. carinata*, shell; (b) *A. bonushenricus*, shell; (c) *A. carinata*, radula: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; (d) *A. carinata*, pseudobranch; (e) *A. carinata*, kidney and renal ridges. a anus; k. kidney; ps.l. pseudobranch lobes; r. rectum; ren. r. renal ridges.

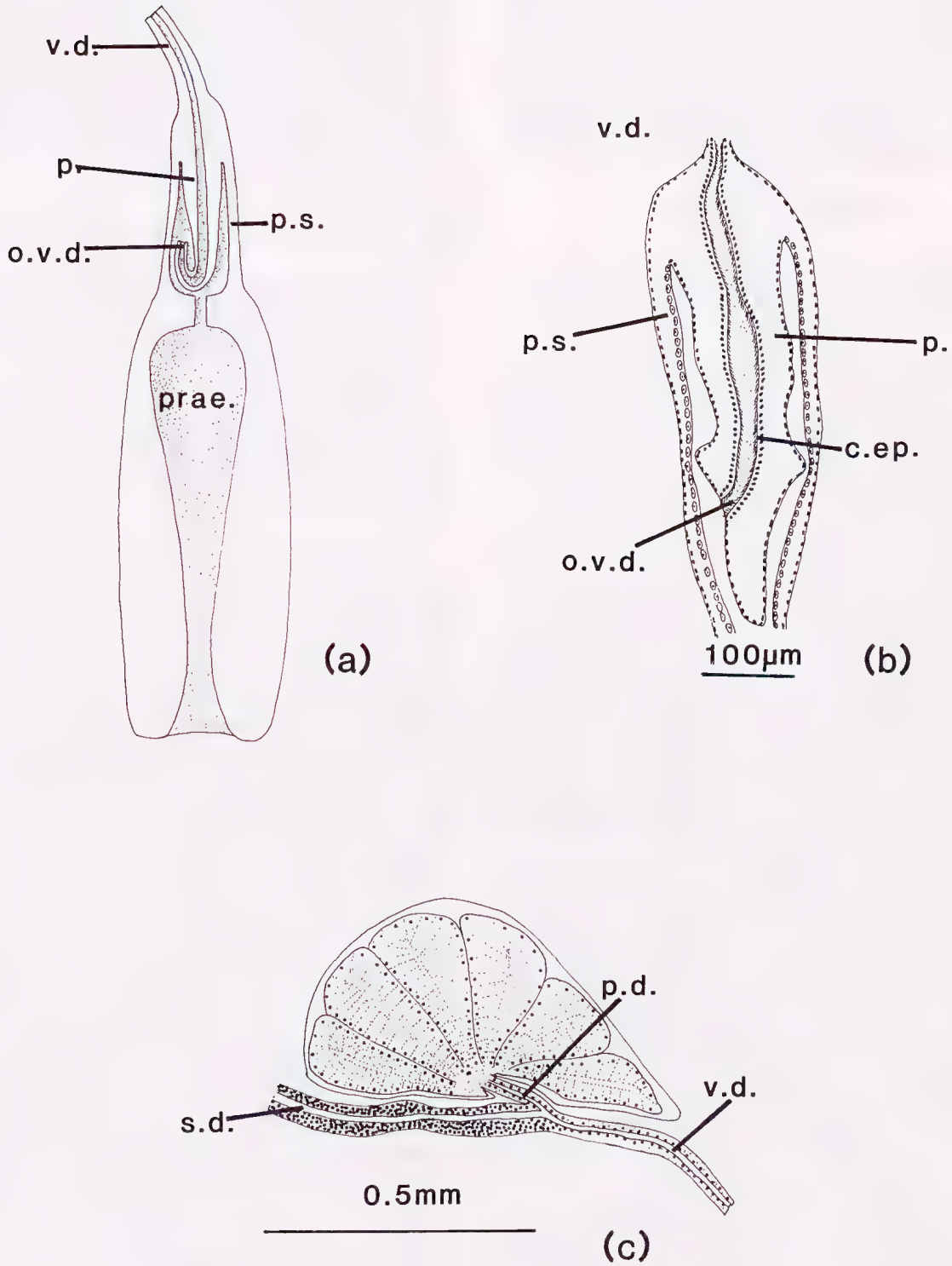


Fig.10. *Amerianna*, continued. (a) *A. carinata*, section of copulatory organ; (b) *Amerianna* sp., Mt. Isa, Qld., l.s., penis; (c) *A. bonushenricus*, prostate gland. c.ep., ciliated epithelium; o.v.d. opening of vas deferens; p. penis; p.d. prostatic duct; prae. praeputium; p.s. penis sheath; s.d. spermduct; v.d. vas deferens.

but at least three, *A. leopoldi*, *A. buruanus* and *A. pesigani*, appear to be valid.

Hubendick (1957) erected the monotypic genus *Patelloplanorbis* for a patelliform freshwater snail from West Irian. The internal anatomy of the type species *P. tigiensis* Hubendick, 1957, is similar to that of *Amerianna*. This is especially true of the pendant penis, which has a terminal pore. Further study is needed to determine the degree of relationship between these genera.

Genus *Bayardella* Burch, 1977

Figs 11, 12

Bayardella Burch, 1977: 80. Type species *Plesiophysa* (*Bayardella*) *johni* Burch, 1977, original designation. Recent, Northern Australia.

Diagnosis. Bulinine snails with neritiform or cylindrical shell with surface having raised spiral ribs and transverse striae; copulatory organ with accessory bursa, lacking flagella, large muscular bulb transversed by duct of accessory bursa and into which penis protrudes is suspended in proximal end of praeputium; anus on anterior edge of rectal lobe.

Description. **SHELL.** Small, sinistral shell, neritiform or cylindrical, with low spire (Fig. 11a,b). Aperture large, oval to pyriform, length almost equal to whole shell, with continuous periostracal fringe; columellar margin reflected and slightly curved without columellar fold; deep umbilicus present. Surface of body whorl with prominent raised spiral ribs and less conspicuous transverse striae, giving appearance of small, incised rectangles.

EXTERNAL MORPHOLOGY. Tentacles filiform. Pseudobranch unilobed or bilobed with secondary folding (Fig. 12a). Rectum opens on anterior edge of rectal lobe. Foot rounded posteriorly.

RADULA. Central teeth with 2 equal or unequal cusps, left cusp often considerably larger, each flanked by a smaller cusp or denticle (Fig. 11c,d). Lateral teeth tricusped with denticles or small cusps between mesocone and ectocone and on lateral edge of mesocone; entocone small, mesocone large, smaller ectocone subdivided into 3 unequal cusps. Transition to marginal teeth involves gradual reduction in size of larger cusps and development of pectinate structure by division of cusps.

SALIVARY GLANDS. Salivary glands tubular; do not pass through circumoesophageal nerve ring (Fig. 12b).

REPRODUCTIVE SYSTEM. Copulatory organ. Accessory bursa arising from top of praeputium (Fig. 12c). Penis sheath narrower than praeputium, approximately $\frac{1}{3}$ as long. Sheath has thin, muscular wall lined internally by simple epithelium of flattened cells with elongate, ovoidal nuclei with scattered chromatin. Penis muscular, with laterally opening vas deferens and minute stylet at tip. Lumen of penis sheath opens into large muscular bulb suspended from proximal end of praeputium. Duct

from accessory bursa enters bulb at level of attachment to praeputium and traverses it vertically, connecting at lower end to duct which is continuous with lumen of penis sheath. Opening of both ducts to lumen of praeputium via branches traversing lower end of muscular bulb (Fig. 12d). Bulb thin walled, containing large sinus formed by splitting of muscle layers. Sinus lacks internal epithelium and is lined by muscle tissue. Epithelium of accessory bursa consists of columnar cells with large, ovoidal, basal nuclei with scattered chromatin (Fig. 12e).

Prostate gland and bursa copulatrix. Prostate gland without prostatic duct. Bursa copulatrix globose.

Distribution. *Bayardella johni* is widely distributed throughout the Kimberley and Victoria River regions of northern Australia. *B. cosmota* occurs in central, eastern and southeastern Australia.

Comments. Several anatomical features point to the unique taxonomic position of *Bayardella*. Hubendick (1955) described the anus of *Plesiophysa ornata* as being posterior to the pseudobranch; that of *Bayardella* opens on the anterior edge of the rectal lobe.

Initial observations (Burch, 1977) indicated that the central tooth of *B. johni* was five cusped, having a single mesocone flanked by two cusps on each side. *Plesiophysa* has a radula with a five-cusped central tooth (Hubendick, 1955). Subsequent studies on the radula of *P. (B.) johni*, using light microscopy (this study) and scanning electron microscopy (Burch & Jeong, 1984), have independently concluded that the original observations were in error. These two studies differ, however, in their interpretation of the nature of the central tooth. Burch & Jeong (op. cit.) describe and figure an asymmetrical central tooth with one major cusp flanked on each side by two unequal cusps or denticles. Apart from the asymmetry, this is similar to the original description by Burch (1977). Some of the material examined in this study was collected at the same time and place as that used by Burch & Jeong (Bow River, Kimberley region, northwestern Australia, 13th May, 1978). Radulae from three separate snails have been examined and teeth have been studied in the intact radula and separated from the radula by long digestion in NaOH. In every case the central teeth have two unequal main cusps, the left cusp being considerably larger, flanked by a smaller denticle (Fig. 12c). Radulae of specimens of *B. cosmota* from Bridgeport in Victoria have central teeth with equal sized cusps, while those from central Australia are similar to those of *B. johni*.

Superficially the copulatory organs of *Bayardella johni* and *B. cosmota* are similar to those described by Hubendick (1967) for some species of *Camptoceras* Benson, 1843. Both genera have an accessory bursa arising from the top of the praeputium. It was a combination of this feature and marked similarity of shell morphology which led

Burch (1977) and Burch & Jeong (1984) to place *Glyptamoda cosmata* into the genus *Camptoceras*. The internal structure of this bursa, revealed in whole mounts and serial sections (Fig. 12 d,e), is markedly different from that of the copulatory organ of *Camptoceras*.

Bayardella and *Camptoceras* differ in several other respects. The pseudobranch of *Bayardella* is a folded structure lying posterior to the anus; the simple,

unfolded pseudobranch of *Camptoceras* lies anterior to the anus (Hubendick, 1967). The nature of the lateral and marginal radula teeth of *Camptoceras* differ from those of *Bayardella* and the salivary glands of *Camptoceras* are globose (Hubendick, 1955), rather than tubular.

Two species, *Bayardella johani* and *B. cosmata*, are recognisable within the genus. They are readily distinguished by shell morphology (Fig. 11a,b).

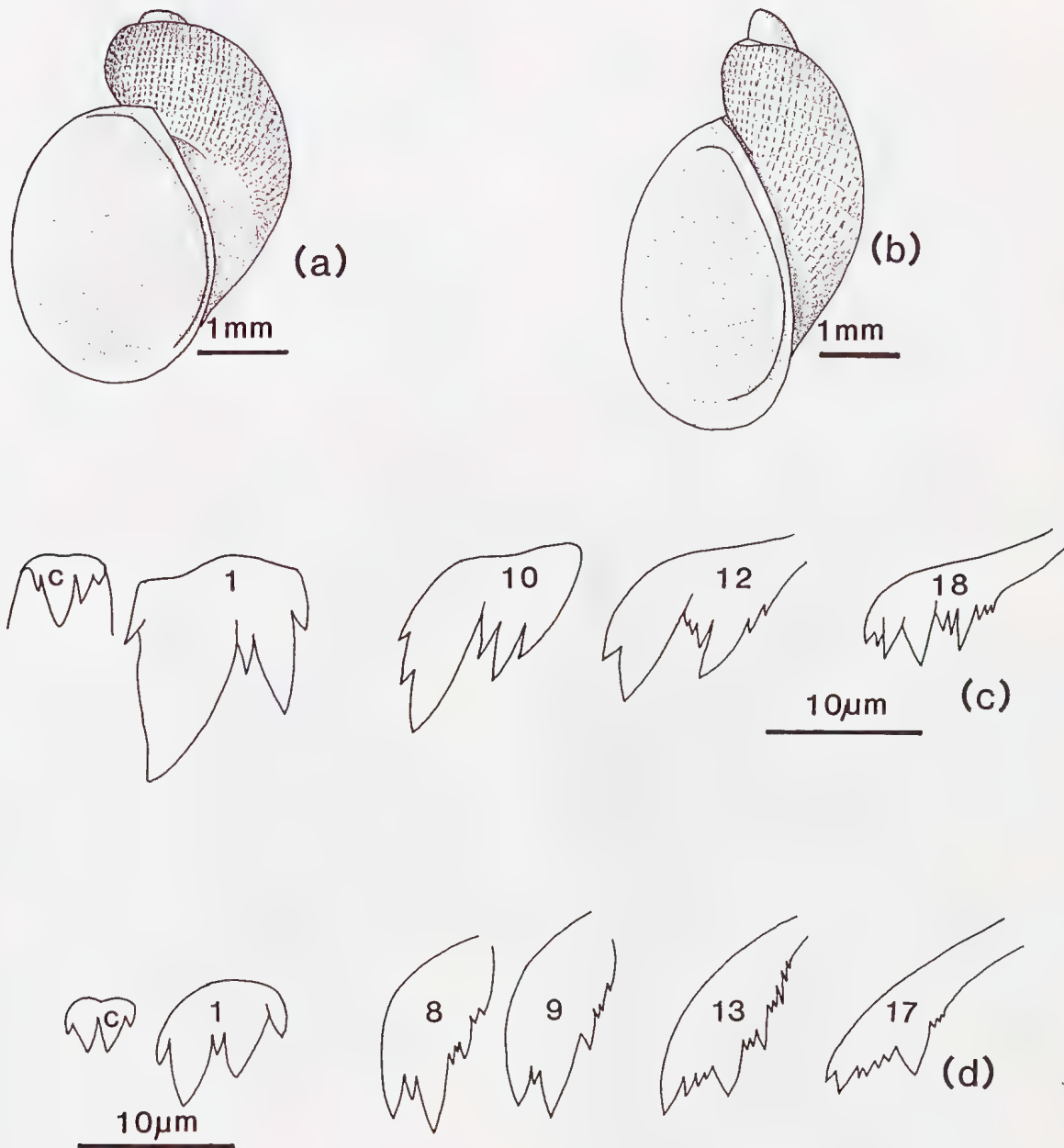


Fig. 11. Anatomy of *Bayardella* (a) shell of *B. johani*; (b) shell of *B. cosmata*; (c) radula of *B. johni*: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; (d) radula of *B. cosmata*.

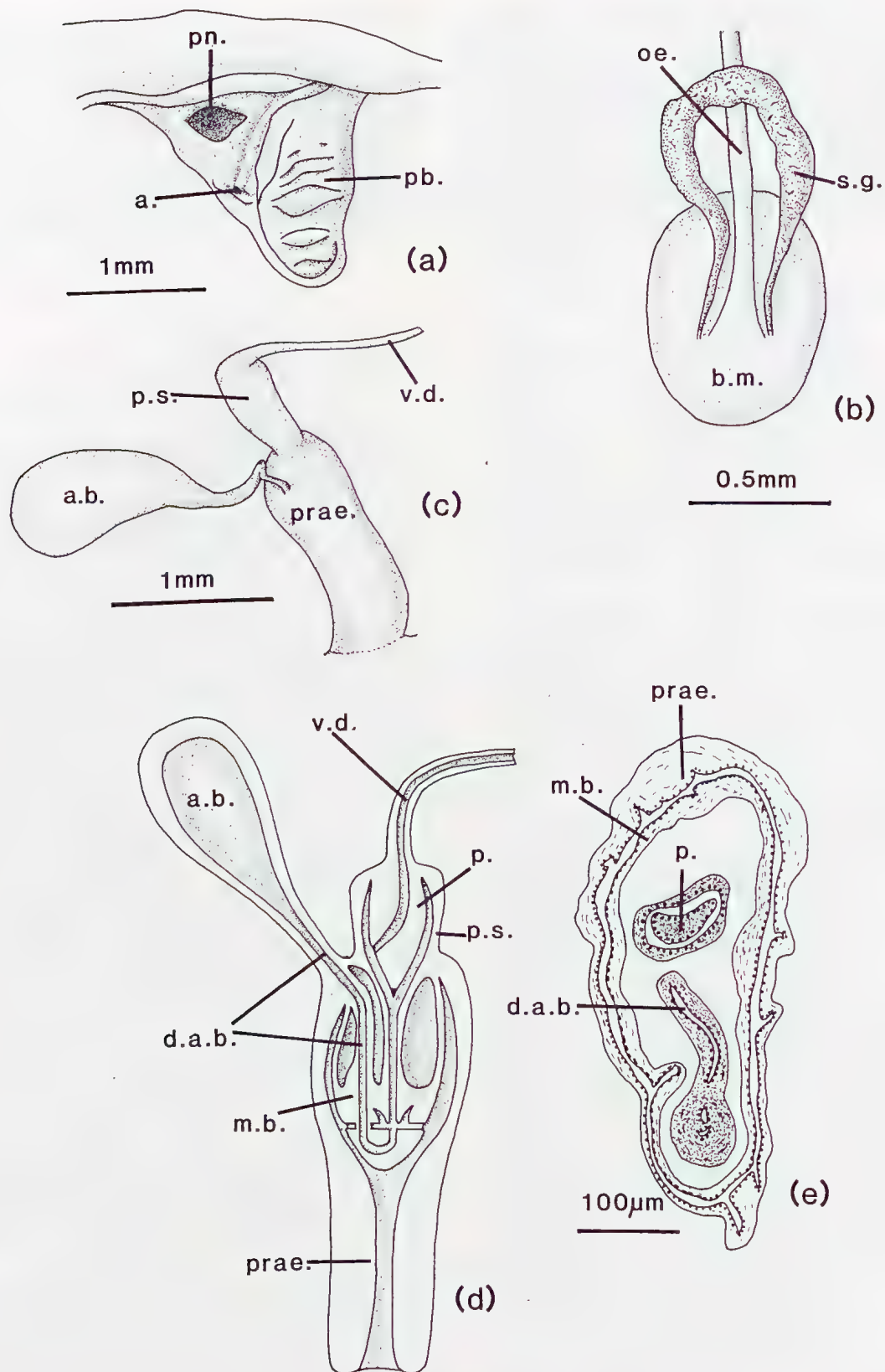


Fig.12. (a) pseudobranch of *B. johni*; (b) salivary glands of *B. johni*; (c) copulatory organ of *B. cosmeta*; (d) copulatory organ of *Bayardella*, diagrammatic view; (e) transverse section through copulatory organ of *B. johni*. a. anus; a.b. accessory bursa; b.m. buccal mass; d.a.b. duct of accessory bursa; m.b. muscular bulb; oe. oesophagus; p. penis; pb. pseudobranch; pn. pneumostome; prae. praeputium; p.s. penis sheath; s.g. salivary glands; v.d. vas deferens.

Genus *Leichhardtia* n.gen.

Fig. 13

Type species. *Bullinus sisurnius* Hedley, 1918. Recent, Paterson Range, Western Australia.

Diagnosis. Bulinine snail having subglobose shell with unshouldered whorls; copulatory organ lacking accessory bursa or flagellum, pendant penis uniramous with lateral pore; prostatic duct present; rectal ridge absent.

Description. SHELL (Fig. 13a). Small (up to about 7mm in length), sinistral subglobose shell; spire depressed, whorls rounded; mature specimens have 3 or 4 whorls; aperture elliptical, parietal lip gently curved, parietal callus adheres to body whorl; umbilicus present; body whorl traversed by spiral rows of striae which bear periostracal hairs in living specimens.

EXTERNAL MORPHOLOGY. Tentacles filiform. Pseudobranch trilobed and secondarily folded, small dorsal lobe projects above level of pneumostome (Fig. 13b). Rectum opens on anterior edge of middle pseudobranch lobe. Posterior end of foot rounded.

RADULA (Fig. 13c). Central tooth with 2 unequal major cusps with minor cusps at base of each. Right cusp usually, but not invariably, longer. Denticle present between major cusps; small denticles on lower lateral edge of right major cusp and occasionally on left. Lateral teeth tricusped with prominent denticles between cusps; first lateral has a single denticle between mesocone and ectocone and small denticles on lateral edge of entocone and on outer edge of base of ectocone. Transition to marginal teeth at about tooth 6; characterised by splitting of entocone into smaller cusps and reduction in size of ectocone. Teeth at extreme margins pectinate.

SALIVARY GLANDS. Salivary glands flat sheets which pass through nerve ring; ducts insert into rear of buccal mass.

MANTLE STRUCTURES. No rectal fold present. Large renal fold on ventral side of kidney (Fig. 13b).

REPRODUCTIVE SYSTEM. Copulatory Organ. Penis is muscular and pendant (Fig. 13d). There are two muscular folds at the distal end (Fig. 13e). Opening of vas deferens is lateral. Praeputium has ciliated epithelium and prominent muscular folds.

Prostate gland. Prostate acini empty into small ciliated ducts which join main prostatic duct.

Bursa Copulatrix. Bursa copulatrix elongate oval. Duct inserts at distal end of vagina.

Distribution. Throughout Kimberley region, into western Northern Territory.

Comments. The differences in copulatory organ structure indicate that Iredale's (1943) placing of *L. sisurnia* in *Lenameria* was incorrect. So too was its inclusion in *Isidorella* by Walker (1984), a decision based on the general similarity of shell morphology and the fact that the complex penis structure of *I. newcombi* could have been derived from that of

Leichhardtia. The nature of the reproductive system, a simple pendant penis and a system of prostatic collecting ducts, suggests some degree of relationship with *Amerianna*. The unequal cusps of the central radula tooth may indicate association with *Bayardella*. The genus is named for Ludwig Leichhardt who made a significant contribution to the exploration of Australia's north.

Discussion

The characters used in assessing the relationships between Australian and African bulniform planorbids are summarised in Table 1. The variability exhibited by these molluscs in shell shape is illustrated by the range of character states which can be applied to a single taxon, reinforcing the conclusion that the shell must be considered of limited value in separating the genera of Australian bulniform planorbids. Of genera described up to the time of Iredale's (1943) checklist and based on shell characters alone, only *Isidorella* remains unchanged. Even with this genus, geographic distribution has unquestionably been important in the retention of a separate identity because of the similarity of these shells to those of African *Bulinus*. In this instance, evidence available from the shell alone would suggest the combining of actually distinct genera. In other instances the reverse is true; anatomical studies have shown that taxa separated on shell characters are congeneric. In the case of *Ancylastrum* the original familial placement has been shown, by anatomical evidence, to be incorrect.

Although many aspects of the anatomy provide useful taxonomic characters, the most consistent differences between groups of species were apparent from studies of the reproductive tract, especially the copulatory organ and prostate gland. This finding is in concordance with that of Hubendick (1955a) in relation to planorbids in general. Apart from the rearrangement of genera based on these criteria, a number of particular points arise.

Most importantly, the use of *Bulinus* as a generic name for freshwater snails from Australia is not justified. From the work of Hubendick (1948a, 1948b, 1955a), and from that of numerous authors since, it is evident that all species of *Bulinus* (and *Indoplanorbis*) have an ultrapenis. No Australian mollusc studied possesses this structure. As mentioned previously, the material on which Hubendick (1948a) based his claim of synonymy between *Bulinus* and *Isidorella* actually came from Lorenzo Marques in Mozambique. It is almost certain that the specimens were of *Bulinus*, either *B. globosus* or *B. africanus*. Hubendick stated that the shell was similar to that of the former and the anatomy to that of the latter. It is stressed that specimens of *Isidorella* from all parts of Australia have been examined in detail and in no instance has a pseudopenis or ultrapenis been found.

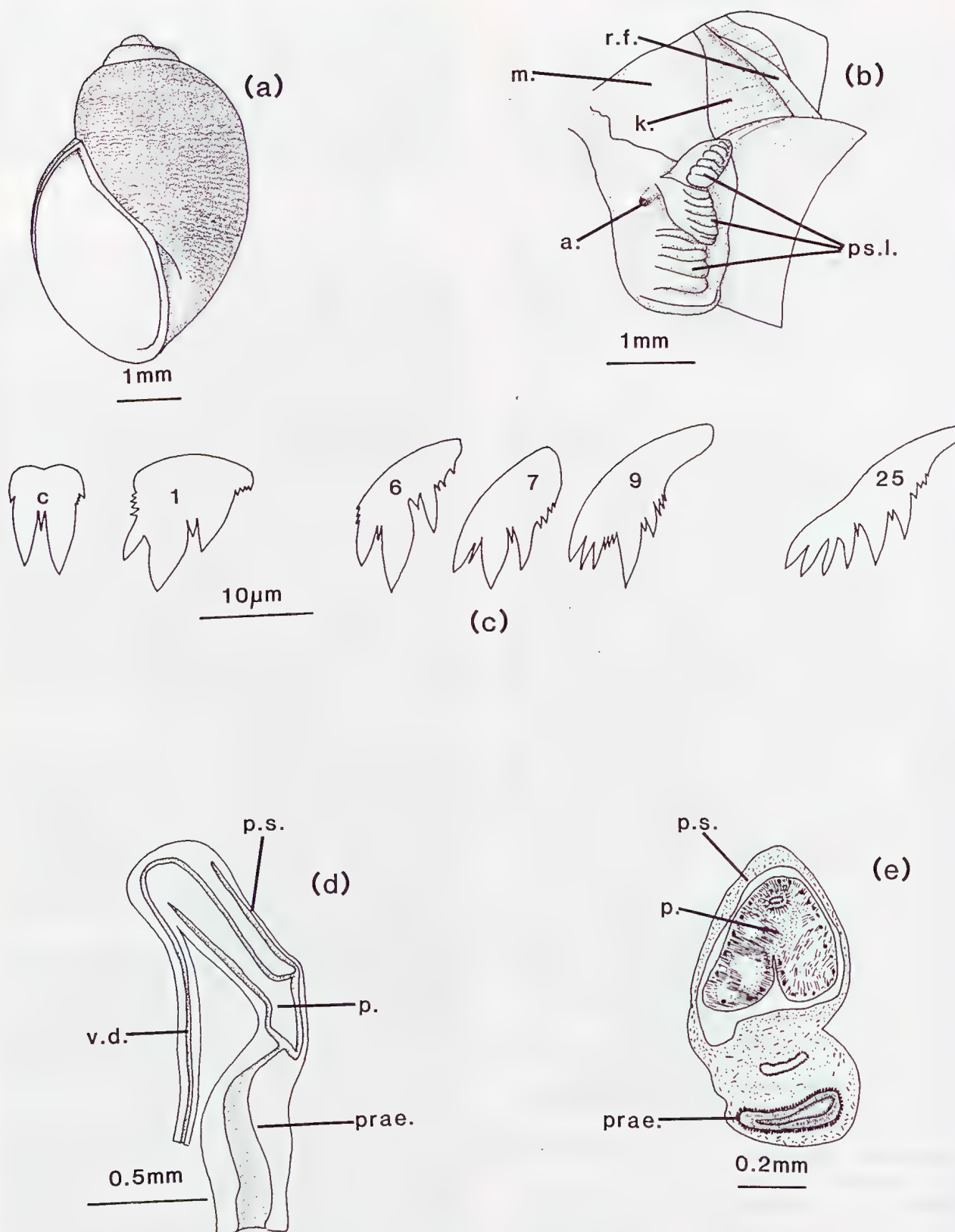


Fig.13. Anatomy of *Leichhardtia sisurnia*. (a) shell; (b) pseudobranch and renal fold; (c) radula: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; (d) copulatory organ, l.s.; (e) copulatory organ, t.s. a. anus; k. kidney; m. inner surface of mantle - folded back; p. penis; ps.l. pseudobranch lobes; prae. praeputium; p.s. penis sheath; r.f. renal fold; v.d. vas deferens.

Wright's (1961) claim that the prostate glands of Australian bulinine planorbids differ from that of *Bulinus* is incorrect, at least for the genera other than *Amerianna* and *Leichhardtia*. The essential details of the glands are similar in both geographic groups. All the Australian bulinine planorbids have prostate glands with the acini branching from a small area of the sperm duct or from a separate prostatic duct. The gonad acini are arranged in a fan-like pattern in all cases. They, therefore, are included in the subfamily Bulininae as defined by Hubendick (1978). This subfamily is wider in definition than the same

author's (1955a) grouping which included only those genera which have an ultrapenis (*Bulinus* and *Indoplanorbis*).

Walker (1984) discussed the geographical relationships of the bulniform planorbids of Australia. Although the classification presented then differs from that presented here in detail (*Leichhardtia sisurnia* is now separated from *Isidorella* and *Physastra* is synonymised with *Glyptophysa*), the general concept of a Gondwanan origin for these snails is still strongly supported.

Table 1. Summary of differences and similarities between genera and subgenera of African and Australian bulniform planorbids.

Key to abbreviations: + = character present; — = character absent; +/- = taxon variable with respect to character; —/+ = character present but slightly developed. (A.c) *Ancylastrum cumingianus*; (A.i) *Ancylastrum irvinae*; (B.c) *Bayardella cosmeta*; (B.j) *Bayardella johni*; (G) *Glyptophysa s.s.*; (O) *G. (Opplatora)*.

	<i>Bulinus</i>	<i>Isidorella</i>	<i>Ancylastrum</i>	<i>Glyptophysa</i>	<i>Amerianna</i>	<i>Bayardella</i>	<i>Leichhardtia</i>
Shell							
globose	+	+		+(O)			
sub-globose	+	+		+(G)			
medium spired	+	+		+(G)		+(B.c)	+
high spired	+			+(G)			
spire truncate	+				+		
carinate	+			+(G)	+		
patelliform			+				
transverse ribs	+		+/(A.i)			+	
spiral lirae	+			+(G)		+	+
peirostracal hairs		+		+/-	+/-		+/-
columellar fold	+			+	-/+		
External Anatomy							
pseudobranch:							
unilobed			+			+(B.j)	
bilobed	+	+		+	+	+(B.c)	
trilobed							+
foot:							
pointed	+	+					
rounded	+		+	+	+	+	+
tentacles:							
long-filiform	+	+		+	+	+	+
short			+				
Internal Anatomy							
radula:							
central tooth							
symmetrical	+	+	+	+	+	—	—
ectocone of 1st							
lateral divided						+	
large rounded							
mesocones			+				
salivary glands:							
tubular and do							
not pass through							
nerve ring						+	
tubular,							
pass through							
nerve ring	+						

flat, branched sheets, pass through n.r.		+	+	+	+		+
rectal ridge	+	—	—	+	+	—	—
renal folds	+ / —	—					—
1 ridge on roof of pulmonary cavity			?	+		—	—
3 ridges on roof of pulmonary cavity	—	—	?	—	+	—	
single fold on ventral side of kidney	+ / —	—	?	—	—	—	+
Reproductive Tract							
copulatory organ:							
accessory							
bursa	—	—	—	—	—	+	—
flagellum	—	—	+	+	—	—	—
penis							
uniramous		—	+(A.c)	+	+	+	+
biramous		+	+(A.i)	—	—	—	—
stylet	—	—	+	+	—	— / +	—
lateral pore		—	+(A.i)	+	+	+	+
terminal pore		—	+(A.c)	—	+	—	—
pseudopenis	+	—	—	—	—	—	—
bursa copulatrix:							
rounded	+	+		+		+	
elongate					+		+
spatulate			+				
prostatic duct	—	—	?	—	+	—	+

Key to the Genera and Subgenera of Australian Buliniform Planorbids

This key is based on the structure of the copulatory organ and on shell morphology.

1. Copulatory organ without an accessory bursa or flagellum. 2
- Copulatory organ with an accessory bursa or flagellum. 4
2. Pendant penis with 2 folded processes. *Isidorella*
- Pendant penis uniramous. 3
3. Shell cylindrical, whorls carinate. *Amerianna* s.s.
- Shell subglobose, whorls with rounded shoulders. *Leichhardtia*
4. Copulatory organ with a muscular flagellum on the proximal end of the penis sheath. 5
- Copulatory organ with an accessory bursa connected to the praeputium. *Bayardella*
5. Penis bilobed or with augur-like folds proximal to the stylet. *Ancylastrum*
- Penis unilobed. 6
6. Shell with a pronounced spire, whorls carinate or with rounded shoulders
..... *Glyptophysa* s.s.
- Shell globose with depressed spire. *Glyptophysa* (*Oppletora*)

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APPENDIX

Snails used in this study have been collected or supplied by various individuals who are listed alphabetically.

A short description of the habitat of each collection site and a list of associated molluscs is given.

List of Collectors and Suppliers of Snails

Name	Affiliation
J.C. Boray (JCB)	Parasitology laboratory, Agricultural Research Station, Glenfield, NSW.
J.B. Burch (JB)	University of Michigan, Ann Arbor, Michigan.
P. Colman (PC)	Australian Museum, Sydney.
P. Davis (PD)	Western Australian Department of Agriculture.
D. Feughelman (DF)	formerly School of Public Health and Tropical Medicine, University of Sydney.
D. McMichael (DM)	formerly Australian Museum, Sydney.
W.F. Ponder (WP)	Australian Museum, Sydney.
C. Roper (CR)	Associate of Australian Museum, Sydney.
R.C. Russell (RR)	School of Public Health and Tropical Medicine, University of Sydney.
B.J. Smith (BS)	National Museum of Victoria, Melbourne.
J. Stoddart (JS)	formerly Western Australian Museum, Perth.
J.C. Walker (JW)	School of Public Health and Tropical Medicine, University of Sydney.
P. Whelan (PW)	Department of Health, Darwin, N.T.

TAXON

Isidorella newcombi s.l.

Colony	Locality collected or origin of sample	Collector	Date
I 1	Suggan Buggan, Vic. 148°20'E;37°00'S, in farm dam	BS	2.4.1972
I 2	Birthday Tank, Sunset, Victoria. 141°30'E;34°56'S.	BS	13.4.1973
I 3	Glenfield, N.S.W. 150°53'E;34°00'S. In stream.	WP	1973
I 4	Coleambally, N.S.W. 145°52'E;34°43'S. In grass filled road-side borrow pit.	JW	Sept, 1973
I 5	Cooma Creek, N.S.W. 149°10'E;36°13'S. Amongst aquatic vegetation at edge of creek.	WP	1973
I 6	Hay, N.S.W. 144°55'E;34°33'S. In low lying land beside road. With <i>Glyptophysa</i> (<i>Physastra</i>), <i>Austropeplea lessoni</i> and <i>Physa</i> sp.	JB/DF	23.9.1975
I 7	Fish River, Oberon, N.S.W. 149°45'E;36°22'S. In water supply tunnel. With <i>Glyptophysa aliciae</i> and <i>G. (Physastra)</i> .	PC	1974
I 8	Great Sandy Desert, W.A. 122°33'E;22°53'S. In rock hole.	JS	26.4.1979
I 9	New Norcia, W.A. 116°13'E;30°59'S.	JS	May, 1979
I 10	Simpson's Gap, Central Australia. 133°43'E;23°42'S. In pools at base of rocks — floating algae	JW/JB	30.5.1979
I 11	Jay Creek, C.A. 133°31'E;23°46'S. In pools in creek bed.	JW/JB	30.5.1979
I 12	Alice Springs, C.A. 133°52'E;23°33'S. In quarry, 20.6 kms north of town.	JW/JB	31.5.1975
I 13	Tephрина Gorge, C.A. 134°19'E;23°31'S. John Hayes Rock Hole, permanent pools in quartzite gorge. With <i>Gyraulus</i> , <i>Petancylus</i> .	JW/JB	2.6.1979

I	14	N'Dhala Gorge, C.A. 134°28'E;23°45'S. In rock pools. With <i>Petanclyus</i> .	JB/JW	2.6.1979
I	15	Serpentine Gorge, C.A. 132°59'E;23°45'S. In rock pools.	JB/JW	3.6.1979
I	16	Glenn Helen, C.A. 132°50'E;23°43'S. In small pool at base of ochre cliff.	JB/JW	3.6.1979
I	17	Hugh River, C.A. 133°20'E;23°46'S. Flowing water, algal covered stones. With <i>Gyraulus</i> .	JW/PC	10.6.1979
I	18	Spencer Gorge, C.A. 133°17'E;23°44'S. Rocky water hole.	JW/PC	10.6.1979
I	19	Hale River, Ruby Gorge, C.A. 134°59'E; 23°29'S. Running water with reeds at edge. With <i>Gyraulus</i> .	JW/PC	13.6.1979
I	20	Paddy's Hole, near Arltunga, C.A. 134°43'E; 23°29'S. Permanent rock pool.	JW/PC	13.6.1979
I	21	Binya, 145°41'E;29°00'S; 112 kms south of Cunnamulla, s.w. Qld. In overflow puddle of trough in bore drain.	CR	7.12.1980
I	22	Rushes Creek, N.S.W. 148°45'E;36°22'S. In vegetation at edge of creek. With <i>Austropeplea tomentosa</i> and <i>Gyraulus</i> .	JW	Dec.1981
I	23	Echuca, Vic. 144°44'E;36°13'S. In irrigation drain.	RR	1982
I	24	Burragate, N.S.W. 149°40'E;36°34'S. In water-cress beds. With <i>A. tomentosa</i> .	JW	13.4.1983
I	25	Bathurst, N.S.W. 149°20'E;33°23'S. With <i>A. tomentosa</i> , <i>G. (Physastra)</i> .	JCB	May 1984

Ancylastrum

Two samples, one of each species of this genus, were available for study. Neither sample had information on habitat or associations with other molluscs.

Ancylastrum cumingianus. 2 specimens, collected by D. McMichael at the southern end of Great Lake, Tasmania, in 1960. From the collection of the Australian Museum, Sydney.

Ancylastrum irviniae. 5 specimens collected by C.E. Beddome, Great Lake, Tasmania, 24.3.1894. From the collection of the Australian Museum, Sydney.

Glyptophysa s.s.

Glyptophysa aliciae

G	1	Fish River, Oberon, N.S.W. 149°45'E;36°22'S. In water supply.	WP	Feb.1975
G	2	Lake Eucumbene, N.S.W. 148°35'E;36°05'S. In streams running into western end of lake.	JW	1976
G	3	Greenbushes, W.A. 116°03'E;33°51'S. In small streams, with <i>Austropeplea lessoni</i> .	PD	15.1.1986

Glyptophysa (Physastra) types

P	1	Inverell, N.S.W. 150°53'E;29°55'S. In water overlying pasture.	JW	Dec.1970
P	2	North Stradbroke Island, Qld. 153°25'E;27°30'S. In swamp at Dunwich.	JW	June 1973
P	3	North Stradbroke Island, Qld. 153°27'E;27°22'S. In roadside ditch at Amity Point.	JW	June 1973
P	4	Torrens River, Adelaide, S.A. 138°35'E;34°55'S.	JW	Sept.1979
P	5	Avondale, Sydney. 151°05'E;33°45'S. In small dam.	JW	Dec.1973
P	6	Casino, N.S.W. 153°02'E;28°40'S.	JB/WP/PC	May 1975
P	7	Proserpine, Qld. 148°35'E;20°21'S.	JB/WP/PC	May 1975
P	8	Fish River, Oberon, N.S.W. 149°45'E;36°22'S.	JW	1975
P	9	Lake Cargellico, N.S.W. 146°24'E;33°18'S. Roadside ditch	JB/DF	22.9.1975
P	10	June, N.S.W. 147°35'E;34°42'S. Roadside ditch. With <i>Physa</i> .	JB/DF	25.9.1975
P	11	Alstonville, N.S.W. 153°30'E;28°50'S.	PC	1975
P	12	Daly River, N.T. 130°35'E;13°45'S. In billabong With <i>Amerianna</i> , <i>Austropeplea</i> .	JB/WP	11.6.1976
P	13	Humpty Doo, N.T. 131°15'E;12°40'S. Fogg Dam at irrigation project. With <i>Gyraulus</i> , <i>Austropeplea</i> and <i>Amerianna</i> .	JB/WP/PC	14.6.1976
P	14	Harrison Dam, Humpty Doo, N.T. 131°15'E; 12°40'S. With <i>Gyraulus</i> , <i>Austropeplea</i> .	JB/WP/DF	16.6.1976
P	15	St. Albans Common, N.S.W. 150°58'E;33°15'S. In swamp.	JW/JS	Jan.1978
P	16	Wyndham, W.A. Parry's Lagoon. 128°15'E;15°32'S. With <i>Austropeplea vinosa</i> , <i>Amerianna carinata</i> , <i>Gyraulus</i> .	JW/JS	7.5.1978
P	17	Palm Valley, Central Australia. 132°40'E;24°03'S. Non flowing water in creek bed. With <i>A. vinosa</i> .	JW/JB	31.5.1979

P	18	Ellery Gorge, C.A. 133°05'E;23°47'S.	JW/JB	3.6.1979
P	19	Ormiston Gorge, C.A. 132°44'E;23°37'S. In water holes at the edge of Ormiston Creek. With <i>Plotiopsis</i> , <i>Petancylus</i> .	JW/JB	3.6.1979
P	20	Hugh River, C.A. 133°20'E;23°46'S. With <i>Gyraulus</i> , <i>Petancylus</i> .	JW/PC	10.6.1979
P	21	Mildura, Vic. 142°10'E;34°15'S.	RR	June 1980
P	22	Burdekin Falls, Qld. 147°09'E;20°39'S.	PC	1981
P	23	Ayr, Qld. 147°15'E;19°33'S. In ponds of sewage treatment works.	PC	1984

Specimens from other sites in Australia and from regions outside Australia. I have examined specimens of *G. (Physastra)* sp. in the collections of the Australian Museum, Sydney, and the National Museum of Victoria, Melbourne. In the latter are many collections from Tasmania, while the former includes specimens from New Zealand, New Guinea, New Caledonia, Tahiti and West Irian. I have also examined specimens from Sorsogon, Philippines.

Glyptophysa (Oppletora) jukesii

GJ	1	Smith Point, Cobourg Peninsula, N.T. 132°10'E; 11°08'S. In lagoon behind Ranger's station. With <i>Gyraulus</i> and <i>Austropeplea vinosa</i> .	JB/WP/DF	1.6.1976
GJ	2	Lagoon, south of Katherine, N.T. Near the King River.	JB/WP/DF	10.6.1976
GJ	3	King Billabong. 130°01'E;15°47'S. Large lagoon with water lillies, beside Victoria Highway, N.T. With <i>Gyraulus</i> and <i>Notopala</i> .	JW/JB	19.5.1978

Amerianna

Amerianna carinata

A	1	Nebo Creek, Qld. 148°41'E;21°41'S.	JB/WP/PC	5.5.1975
A	2	Humpty Doo, N.T. 131°51'E;12°40'S. Fogg Dam, at irrigation project. With <i>A. vinosa</i> , <i>G.(P) concinna</i> and <i>Gyraulus</i> .	JB/WP/DF	16.6.1976
A	3	Cheese Tin Creek, Kununurra, W.A. 128°16'E;15°42'S. In isolated pools in the bed of drying stream. With <i>Bayardella johnei</i> , <i>Gyraulus</i> , <i>Petancylus</i> .	JW/JS	7.5.1978
A	4	Lake Argyle, W.A. 128°50'E;16°20'S. In lagoon near Spillway Creek. With <i>A. vinosa</i> .	JB/JW/JS	9.5.1978
A	5	Hidden Valley, Kununurra, W.A. 128°45'E;15°43'S. With <i>A. (Ameriella) sisurnia</i> .	JW/JB	14.5.1978
A	6	Mount Isa, Qld. 139°30'E;20°43'S. In dam.	JW	1980
A	7	Darwin, N.T. 130°52'E;12°28'S. In small creek. With <i>A. vinosa</i> .	PW	29.6.1984

Amerianna bonushenricus

A	8	Bow River. 128°07'E;17°15'S. On stones in isolated pools in river bed. With <i>B. johnei</i> , <i>Gyraulus</i> , <i>A. vinosa</i> , <i>Petancylus</i> and <i>Notopala</i> .	JW/JB/JS	13.5.1978
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Bayardella

Bayardella johnei

Bj	1	Bell Creek Crossing, King Leopold Ranges, W.A. Collected by B.J. Wilson and S. Slack-Smith.	JS	27.8.1975
Bj	2	Kununurra W.A. 128°10'E;15°42'S. In pools in bed of Cheese Tin Creek. With <i>Gyraulus</i> and <i>Petancylus</i> .	JW/JS	7.5.1978
Bj	3	Bow River, W.A. 128°07'E;17°15'S. On stones in isolated pools in river bed. With <i>A. (Ameriella) bonushenricus</i> , <i>Gyraulus</i> , <i>Austropeplea vinosa</i> , <i>Petancylus</i> and <i>Notopala</i> .	JW/JB/JS	13.5.1978

In addition to these samples, I have also examined the type specimens in the collections of the Australian Museum, Sydney. This also applies to the second species of this genus, *B. cosmata*.

Bayardella cosmata

Bc	1	Bridgewater, Vic. 143°58'E;36°36'S. Aestivating on sticks and bark beside the Loddon River. This material is in the collection of the National Museum of Victoria, Melbourne.	BS	16.5.1973
Bc	2	Palm Valley, C.A. 132°44'E;24°02'S. In a small pool in the bed of a south flowing tributary of Palm Creek. On algal covered leaves and rocks.	JW	9.6.1979

Leichhardtia
Leichhardtia sisurnia

L	1	Hidden Valley, Kununurra, W.A. 128°45'E;15°43'S. Small pool with stones, gravel bottom, filled by runoff. With <i>A. carinata</i> .	JW/JB	14.5.1978
L	2	Kununurra, 129°02'E;16°00'S. In small creek beside Duncan Highway. 43km sth of Kununurra.	JB/JW	16.5.1978
L	3	Jasper Creek, 130°41'E;16°03'S. Pond filled with aquatic vegetation beside Top Springs-Timber Creek road, N.T.	JB/JW	19.5.1978

I have examined the type specimens of *Leichhardtia sisurnia* in the collection of the Australian Museum, Sydney.

Other planorbids used in this study

In addition to the Australian species listed above, I have had material of two genera, *Bulinus* and *Indoplanorbis* for comparative studies. This material was: *Bulinus truncatus* from Egypt, *Bulinus tropicus* from Rhodesia, *Bulinus sericinus* from Ethiopia, and *Bulinus octoploidus* from Ethiopia, all supplied by Professor J.B. Burch. In addition I had available a colony of *Indoplanorbis exustus* collected by Professor Burch in Madras, India, in 1979. *Bulinus (Physopsis) globosus* collected in NW Liberia by W. Hofler and H.J. Knuttgen on 4.5.1975. These fixed specimens, from a laboratory colony, were supplied by Dr. C.M. Meier-Brook, Tropenmedizinisches Institut, University of Tübingen.

The Genera *Bembicium* and *Risellopsis* (Gastropoda: Littorinidae) in Australia and New Zealand

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ABSTRACT. The taxonomy of the Australasian littorinid genera *Bembicium* and *Risellopsis* is revised. Five Recent species of *Bembicium* are recognised: *auratum*, *nanum*, *melanostoma*, *vittatum* and *flavescens*, the first four of which occur on the Australian mainland, the last on Norfolk and Lord Howe Islands. *B. melanostoma*, *B. vittatum* and *B. flavescens* are sibling species which have been synonymised as *B. melanostoma* in recent systematic accounts, and are shown to be allopatric and distinguished mainly by characters of the penis. At least three fossil species of *Bembicium* are known, of which one is described as new, and the fossil record extends back to the late Oligocene or early Miocene. The genus is endemic to Australasia and presently extinct in New Zealand and the Kermadec Islands. The genus *Risellopsis* is monotypic, represented only by *R. varia* in New Zealand, and has no fossil record before the Pleistocene. Systematic descriptions of the shell and animal and details of habitat and distribution are given for each species. These genera are abundant in the intertidal zone and the rather large literature on their biology and ecology is reviewed. Relationships with other littorinacean taxa are discussed. It is suggested that *Bembicium* and *Risellopsis* together form a monophyletic group, defined by synapomorphies of anterior salivary glands, anterior position of the junction of the duct of the seminal receptacle with the pallial oviduct, longitudinal division of the jelly gland and trochoidal shell shape. The littorinid genus *Peasiella* is superficially similar in shell characters, but anatomical features show that it is not closely related to *Bembicium* and *Risellopsis*. Interesting features of *Bembicium* include the type of development (the hatching of planktotrophic veligers from benthic egg masses recorded in two species is rare in the family) and the extreme intraspecific variability in the form of the radular teeth.

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The genus *Bembicium* comprises a small group of littorinacean gastropods with characteristically trochoidal shells, which occur only on the coasts of Australia and adjacent islands. *Risellopsis* is represented by a single species from New Zealand, and has long been recognised as a close relative of *Bembicium*. All species are common in the intertidal zone, and some have been the subject of a considerable amount of ecological research. The most recent taxonomic treatment of *Bembicium* was by H. Anderson (1958), but this work provided very little anatomical information, and was based largely upon specimens from South Australia.

Recently the taxonomy of a number of littorinid groups has been reevaluated on the basis of new anatomical evidence (Fretter & Graham, 1980; Mastro *et al.*, 1982; Bandel & Kadolsky, 1982; Reid, 1986). A preliminary analysis of phylogenetic relationships within the Littorinidae has suggested that *Bembicium* may be an early offshoot retaining a number of ancestral characters (Reid, 1986), while other authors have proposed its separation as a distinct family. In the present account, anatomical studies of *Bembicium* and *Risellopsis* have been used both to reconsider the species-level taxonomy, and to provide further information about the relationships of these genera with others in the family. A cladistic analysis of the relationships of littorinid genera is in preparation, and a detailed discussion of phylogeny will be deferred. An additional problem in the past has been confusion of *Bembicium* with the superficially similar littorinid genus *Peasiella*, and the mistaken assumption of a close relationship

between the two. These genera have now been clearly defined, permitting a reconsideration of the fossil record and biogeography of *Bembicium*.

Taxonomic History

In view of the trochoidal shape of the shell of *Bembicium*, it is not surprising that early authors included species in the genus *Trochus* (Gmelin, 1791; Dillwyn, 1817; Lamarck, 1822; Wood, 1828; Quoy & Gaimard, 1834). This practice was occasionally continued even after the littorinid affinity of the shells was recognised (Reeve, 1842 a,b; Deshayes & Milne Edwards, 1843; Philippi, 1843; Gould, 1852). Although Quoy & Gaimard (1834) used the generic name *Trochus*, they recognised that the separate sexes, paucispiral operculum and lack of epipodial tentacles set the animals apart from typical members of the genus, and therefore included them (with *Trochus* [= *Tectarius*] *pagodus* Linnaeus) in a separate, but unnamed, section.

The first author to group species now classified as *Bembicium* with other littorinids was Gray, who in 1839 described two new species in the genus *Littorina*, and noted that because of their shell shape they would probably form a new section. The generic name *Risella* was listed the following year, without diagnosis or included species, in both versions of edition 42 of the *Synopsis of the Contents of the British Museum* (Gray, 1840a, b; see Iredale, 1913). Although in these first usages the genus was a *nomen nudum*, a brief diagnosis was given in edition 44 of the *Synopsis*: '*Risella* is like *Littorina*, but the shell is

top-shaped, the whorls keeled, and the mouth rather square' (Gray, 1842: 60). Iredale (1913) advocated rejection of all the names introduced in this edition, but nevertheless the diagnosis is adequate to define the genus, so that the name *Risella* must take the date of 1842. The type species, *Trochus melanostoma* Gmelin, was subsequently designated by Gray (1847).

The name *Bembicium* was introduced by Philippi (1846) for species with a trochoidal shell and animal like *Littorina*, but differing from *Trochus* in the lack of frontal lobes, of epipodial tentacles and of a multispiral operculum, and in the non-nacreous shell. Herrmannsen (1846) designated *Trochus melanostoma* Gmelin as the type species. The priority of *Risella* was recognised by Philippi (1851, 1853), and thereafter this generic name came into general usage (e.g. Adams & Adams, 1858; Crosse, 1864; Angas, 1865; Fischer, 1879; Tryon, 1887; Kesteven, 1903), although Tenison-Woods (1879) chose to retain *Littorina*. However, in 1912 Iredale reinstated the name *Bembicium*, overlooking Gray's (1842) diagnosis of *Risella*, and claiming that the earliest available introduction was that of Gray (1847). Almost all subsequent workers followed Iredale (1912), although the name *Risella* occasionally appeared in the palaeontological literature (e.g. Speight, 1913; Cossmann & Peyrot, 1918). Despite the priority of *Risella*, it is clear that, pending application to the ICZN for suppression of the name, nomenclatorial stability can best be served by maintaining the existing usage of *Bembicium* (ICZN, 1985, Articles 23b, 79c).

The taxonomic history of *Risellopsis varia* (Hutton) is similar to that of *Bembicium* species, having been described in the supposedly trochid genus *Adeorbis* (Hutton, 1873), then grouped with other littorinids, first tentatively as a *Risella* (Hutton, 1878), then as a *Fossarina* (a genus now placed in the Trochidae, but see Kesteven, 1902, for a discussion of an error in the original description by Adams & Angas, 1863; Hutton, 1880, 1882). Kesteven (1902) recognised the close relationship with *Risella* (= *Bembicium*), but created the new genus *Risellopsis* because of differences in the shell and radula. Subsequent workers have followed this classification.

Several authors have considered *Bembicium* and *Risellopsis* sufficiently distinct from other littorinids to be assigned to a separate family. Kesteven (1903) created the Risellidae on the basis of the closed pallial vas deferens and penial sperm duct, and presence of an ovipositor. All three characters can, however, be found in certain members of the Littorinidae, and the retention of the two genera in this family will be discussed further below. Finlay (1928) renamed the supposed family Bembiciidae. Separate familial status has not received general acceptance by later authors, with some exceptions (Odhner, 1924; Cotton & Godfrey, 1938;

Macpherson & Chapple, 1951; Kershaw, 1955). Rosewater (1970) considered *Bembicium* and *Peasiella* 'at least a separate subfamily' of the Littorinidae. Many *Peasiella* species were initially described in the genus *Risella*, but despite a superficial resemblance between the shells, the two groups are not now thought to be closely related (Reid, 1986).

At the specific level, variability in shell characters in the genus *Bembicium* is so great that opinions on the classification of the species have differed considerably. A total of 21 names are available for the Recent species, 19 of which were described between 1828 and 1866. In 1834, Quoy & Gaimard classified the forms from the Australian mainland and Tasmania into four species: *luteus* (includes two species as defined in the present revision, separable only by anatomical characters), *nanus*, *planus* (here regarded as juvenile *B. nanum*) and *auratus*, and so came close to the system proposed here. In a monograph of *Bembicium*, Philippi (1846) took more account of variation in shell form, and accepted eight species, to which he later added four more (Philippi, 1851). This made a total of 12, which were finely illustrated in a second monograph (Philippi, 1853). Crosse (1864) produced a third monograph, and with a similar species concept to that of Philippi, enumerated nine species (making no reference to Philippi, 1851 or 1853). Smith (1884) made some attempt to synonymise, but still accepted at least six species. The first suggestion that only one variable species was involved was made by Tenison-Woods (1877, 1879), who also made the extraordinary assertion that though all animals were hermaphrodite, *Risella aurata* functioned as the male and *R. nana* as the female. The concept of a single variable species was maintained by Tryon (1887), Pritchard & Gatliff (1902), Kesteven (1903) and Hedley (1910, 1916, 1918). Other Australian authors have mostly adopted a classification similar to that of Quoy & Gaimard (1834), accepting two or three species in New South Wales (Angas, 1867; Musgrave, 1929; Iredale, 1931; Iredale & McMichael, 1962), two or three in Tasmania (May, 1921, 1923; Kershaw, 1955), four in Victoria (MacPherson & Chapple, 1951) and three to five in South Australia (Angas, 1865; Verco, 1908; Cotton & Godfrey, 1938). The details of the species concepts of these authors may be found by reference to the synonymies in the systematic section.

Since 1958 the basis for the modern classification of the species of *Bembicium* has been the revision by H. Anderson. In defining species, Anderson placed most emphasis on characters of the shell, and using material largely from South Australia, she recognised three species: *B. melanostoma*, *B. auratum* and *B. nanum*. This conclusion was supported by a study of the egg masses of the first two, and by limited anatomical descriptions. The presence of three species in South Australia is confirmed by the

present study. However, Anderson's concept of *B. melanostoma* has been modified by its exclusion from the faunas of Queensland and New South Wales, and by its division into two conchologically similar, but anatomically distinct, species: *B. melanostoma* s. s. from Victoria and Tasmania and *B. vittatum* from South and Western Australia. The concepts of *B. auratum* and *B. nanum* remain unchanged, but an additional species, *B. flavescens*, is recognised from Norfolk and Lord Howe Islands.

Despite the work of H. Anderson (1958), there has still been confusion of the identity of the *Bembicium* species. Although *B. nanum* is distinctive, *B. auratum* and *B. 'melanostoma'* have often been misidentified in museum collections, perhaps because the latter is usually the more golden in colouration, while the former frequently has a black aperture.

Materials and Methods

This taxonomic work has been based largely upon the collections of the following institutions: Australian Museum, Museum of Victoria, South Australian Museum, Western Australian Museum, National Museum of New Zealand, New Zealand Geological Survey, British Museum (Natural History), Muséum National d'Histoire Naturelle (Paris) and National Museum of Natural History (Washington).

Except where otherwise stated in the synonymies, all available type material has been examined. The types of the species described by Philippi (1846, 1851) are not located in either the British Museum (Natural History) or the Museum für Naturkunde, East Berlin (R. Kiliyas, pers. comm.), nor could information be obtained about their possible presence in the Museo Nacional de Historia Natural, Santiago, Chile. The figures published by Philippi in 1853 have therefore been designated as lectotypes.

Only taxonomic, faunistic and anatomical works have been listed in the synonymies; references to ecological studies are given in the introductory sections.

Measurements were made of adult shells, which showed a slightly thickened and non-growing apertural lip. Shell height was measured parallel to the axis of coiling, and shell diameter as the maximum dimension perpendicular to the axis. The height/diameter ratio was calculated as a measure of shell shape. The number of whorls of the teleoconch was counted from the slight ridge terminating the protoconch, or, if the apex was eroded, by comparison with well-preserved juveniles from the same locality. The number of whorls of the protoconch was counted by constructing a line tangential to and a continuation of the tip of the sutural spiral, and counting three-quarters of a whorl the first time the sutural spiral crossed the line, and an additional one whorl for each subsequent

intersection, with the final whorl estimated as a fraction of a revolution. For example, the protoconch illustrated in Fig. 14d has 1.5 whorls. This method gives results similar to that described by Jablonski & Lutz (1980), but is more accurate, since it defines precisely the extent of the first whorl.

Preserved material in museum collections was used for anatomical studies. From the observation of living animals of *Bembicium nanum* and *B. auratum* at Sydney, New South Wales, and Magnetic Island, Queensland, it appears that the shape of the penis of preserved animals is very similar to that in the living state. Drawings of penes and pallial oviducts were made using a camera lucida, from animals with mature gonads showing no evidence of parasitism by trematodes. The complex structure of the pallial oviduct was investigated both by serial histological sectioning and by cutting gross serial transverse sections under a dissecting microscope. For each species the reproductive anatomy was examined in ten to 30 males and five to ten females, from the widest available range of localities.

Serial histological sections were cut of a single mature penis of each species, of two pallial oviducts of *B. auratum*, and one each of *B. nanum* and *Risellopsis varia*. Sections were cut at 5 µm and were stained using either Masson's trichrome (Luna, 1968) or the alcian blue-periodic acid-Schiff technique for the histochemical differentiation of mucins (Sheehan & Hrapchak, 1973). The latter stains acidic mucins blue and neutral mucins magenta, while mixed mucins appear purple.

Spermatozoa were examined from two specimens each of *B. auratum* and *B. nanum* from North Harbour, Sydney, and *B. auratum* from Magnetic Island, Queensland. Samples were removed from the seminal vesicle of living, mature, unparasitised males, and fixed in a 1% solution of glutaraldehyde in sea water before examination with a light microscope.

The radulae of five, and in the case of *B. auratum* ten, specimens of each species were examined with a scanning electron microscope. The specimens used were mature examples of both sexes, from a wide geographical range. Radulae were treated with hot 50% potassium hydroxide solution for 15 minutes, rinsed, cleaned ultrasonically for ten seconds, and mounted flat. Although side and top views of some species are also shown, the standard view adopted for showing the shape of tooth cusps was from the posterior end at an angle of 45° to the horizontal. Only teeth from the central region of the radular ribbon were photographed. The total length of each intact radula was measured, and its relative length recorded as the ratio of total length to shell diameter.

Comparisons with other littorinid genera are based on published accounts as quoted, on the species listed by Reid (1986, pp. 5–6) and on new observations of *Mainwaringia leithii* and *Lacuna vineta* (Reid, in prep.).

The locality records are not complete lists of all material examined, but are lists of only those records plotted on the distribution maps.

Abbreviations

ABPAS	Alcian blue – periodic acid – Schiff stain
AIM	Auckland Institute and Museum
AMS	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
DGR	Collection by author, material now in BMNH
MHNG	Muséum d'Histoire Naturelle, Geneva
MNHNP	Muséum National d'Histoire Naturelle, Paris
MT	Masson's trichrome stain
NMNZ	National Museum of New Zealand, Wellington
NMV	Museum of Victoria, Melbourne
NZGS	New Zealand Geological Survey, Lower Hutt
SAM	South Australian Museum, Adelaide
TM	Tasmanian Museum, Hobart
USNM	National Museum of Natural History, Washington, D.C.
WAM	Western Australian Museum, Perth
ZMB	Museum für Naturkunde, East Berlin

SHELL CHARACTERS

Shape, size and sculpture. The keeled, trochoidal shape of *Bembicium* and *Risellopsis* is unusual in the family Littorinidae, being seen elsewhere only in *Peasiella*. The similarity is superficial, however, and *Peasiella* is not closely related. It is not clear why shell shape should be convergent in the two groups. Another unusual feature of *Bembicium* is the presence of a thickened spiral ridge within the aperture, parallel to and just below the peripheral keel (Tenison-Woods, 1877), although this is indistinct in juveniles. Shell growth in *Bembicium* and *Risellopsis* is allometric, the apical angle decreasing with size, so that the spire outline is convex or domed. This is most striking in shells lacking strong radial sculpture, such as *B. nanum* and smooth forms of *B. melanostoma* and *B. vittatum*. Juveniles of *B. nanum* are so much flatter in appearance than adults that they have often been regarded as a separate species, *B. planum* (e.g. Quoy & Gaimard, 1834; Philippi, 1846, 1853; Cross, 1864; Cotton & Godfrey, 1938; MacPherson & Chapple, 1951). The positive allometry of shell height on shell diameter is illustrated graphically in Fig. 1 for a sample of *B. nanum* from Jervis Bay. The phenomenon of doming is common in other littorinids and in gastropods in general (Vermeij, 1980).

The attainment of adult size is not marked by any change in the shape of the aperture, but only by a

slight thickening of the margin when growth slows or ceases. Variation in adult shell size within species is considerable, most showing an approximately two-fold range, and may sometimes be correlated with geographical distribution. Sexual dimorphism has often been reported in littorinids, females being somewhat larger (Reid, 1986). The dimorphism is only slight in *Bembicium* species; for example, the mean diameter of 15 adult male *B. auratum* from Cockle Bay, Magnetic Island, Queensland, was 13.3 mm, and of 13 females 14.2 mm ($t = 2.48$, $P = 0.021$). The larger size of females may be explained by their higher growth rate (Muggeridge, 1979).

Shell shape and sculpture show great variation in both *Bembicium* and *Risellopsis*, as illustrated in the systematic section. As an example, the shell height/shell diameter ratio of *B. auratum* ranges from 0.639 to 1.483, the peripheral keel may be weak or flanged, straight or undulating, the radial folds may be absent or strongly developed (Fig. 16). Much of this variation is on a geographical scale, variation within populations at single localities being much less. *B. auratum*, for example, has a distinctive form in north Queensland. Amongst European *Littorina* species, those with direct, nonplanktotrophic development show a greater degree of interpopulation variability in shell size, shape and sculpture than those with planktonic veliger larvae. The restricted dispersal of nonplanktotrophic species permits adaptation to local conditions of predation and exposure to wave action (review by Raffaelli, 1982). Even in planktotrophic littorinids, selection may maintain striking differences between populations (Struhsaker, 1968). No similar studies of variation in *Bembicium* or *Risellopsis* have yet been carried out. *B. vittatum* is believed to undergo direct development (H. Anderson, 1958), and limited museum collections show that it is a variable species, although not more strikingly so than *B. auratum* with planktonic veligers. Although it may seem superficially that intraspecific variation is comparable with or exceeds interspecific variation in *Bembicium*, three of the five species can usually be identified on the basis of shell characters, of which the number of spiral grooves above the periphery, the number of ridges on the base, and the apertural colouration are most important. *B. melanostoma* and *B. vittatum* are commonly identical and separable only by using anatomical or distributional data.

In addition to the spiral ridges and grooves, both *Bembicium* and *Risellopsis* bear a fine microsculpture of spiral striae. In *Bembicium* the striae are at first parallel to the major grooves, but become somewhat oblique by the last whorl. In many specimens microsculpture, and even the major grooves, may be obscured by erosion. The periostracum of *Bembicium* species is not noticeable. In small or well-preserved shells of *Risellopsis* the periostracum may be produced into pointed bristles 0.2 mm long on the ribs, and are especially

conspicuous on the base (Fig. 26a). This character is unusual in littorinids, but is also known in *Littoraria vespacea* Reid, *Peasiella isseli* (Semper in Issel) and *Mainwaringia leithii* (Smith), a diverse group not sharing close relationship.

Protoconch. Shells of *Bembicium* and *Risellopsis* are usually eroded, so that it is rare to find specimens with intact apices. Protoconchs have been examined in only one example of each of four species of *Bembicium* and two of *B. auratum*. In these

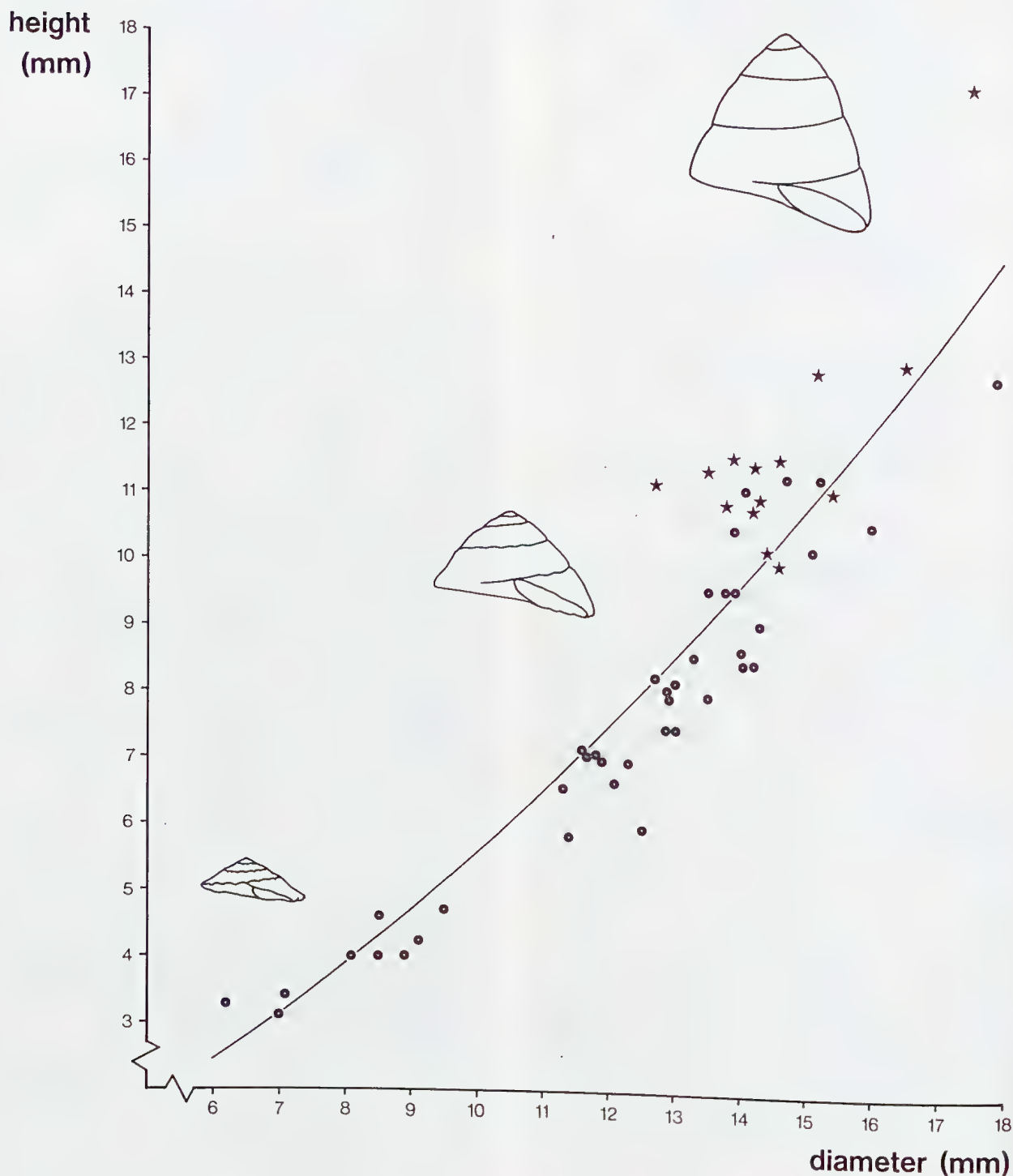


Fig.1. Allometry in shell growth of *Bembicium nanum* (Lamarck) from Honeymoon Beach, Jervis Bay, N.S.W. (AMS C144329). Fitted curve has the equation: height = 0.130 (diameter)^{1.63} ($r^2 = 0.90$; 95% confidence limits of exponent = 1.48–1.78). Solid circles indicate shells with a thin, growing edge to aperture; asterisks are adult shells.

specimens the protoconch is low, only slightly protruberant, of 1.25 to 1.5 whorls, and measuring 0.35 to 0.45 mm in diameter. Protoconch stages I and II (Jablonski & Lutz, 1980) cannot be distinguished, for the surface is smooth, but for traces of radial growth striae close to the terminal lip. The lip itself is no more than a strong growth line, not raised or ornamented; in *B. auratum* (Fig. 17d) it is indented by a curvature, and this is more conspicuous in *B. nanum* (Fig. 22d), while in *B. melanostoma*, *B. vittatum* (Fig. 11a) and *B. flavescens* (Fig. 14d) the edge of the lip and the growth striae behind it are almost straight.

It is well known that the type of larval development is reflected in the form of the protoconch. In littorinids with pelagic egg capsules and an estimated planktonic larval life of four to eight weeks, the protoconch is 0.25 to 0.45 mm in length, of 2 to 3.5 whorls, sculptured by spiral ribs or rows of tubercles, and terminated by a strong sinusigera rib (e.g. Struhsaker & Costlow, 1968; reviews by Bandel & Kadolsky, 1982, and Reid, 1986). In contrast, lecithotrophic species lacking a planktonic stage have a protoconch of less than 2 whorls, approximately 0.40 to 1.49 mm in diameter, with a straight lip lacking any trace of a sinusigera rib (Thorson, 1946; Bandel, 1975; Picken, 1979; Rosewater, 1982). The protoconchs of *Bembicium* species agree well with the available information on their life histories, as reviewed below. *B. nanum* and *B. auratum* develop in benthic egg masses and hatch as veligers (D.T. Anderson, 1961, 1962); the form of the protoconch suggests that the period of planktonic life may be short. *B. vittatum* is believed to lack a planktonic stage (H. Anderson, 1958), and the protoconchs of *B. melanostoma* and *B. flavescens* suggest that direct development may occur in these species also.

The protoconch of *Risellopsis varia* has not been seen, but veligers from the plankton with unsculptured shells of up to 1.5 whorls and 0.45 mm diameter, lacking a sinusigera notch, have been tentatively identified as belonging to this species (Pilkington, 1976).

Colour. Shell colouration in *Bembicium* is rather ill defined, both because shells are frequently eroded, and also because of the range of variation within species. In each species the palest specimens bear only a faint speckling of brown pigment on a white to cream ground colour, while the darkest show conspicuous axial stripes of dark brown to black, corresponding with either the ribs or folds of the axial sculpture. In all species spots may be present or absent on the base. The dark brown colour of the outer wall of the aperture, often in combination with an orange columella, is useful for defining the 'melanostoma' group (*B. melanostoma*, *B. vittatum*, *B. flavescens*). Apertural colouration in *B. auratum* is more variable, usually with a few broad black stripes at the margin of the outer lip, but commonly entirely

white in specimens from north Queensland. Only in *B. nanum* is shell colouration virtually diagnostic, the pattern of narrow black stripes on the dorsal surface, which forms four to ten short stripes inside the outer edge of the aperture, being distinctive. In *Risellopsis* the colour pattern is also primarily of radial stripes on the dorsal side, but in combination with more or less distinct spiral lines in the grooves of the spiral sculpture. In all species variation in colour appears to be continuous, and no discrete morphs can be recognised.

Operculum. The opercula of the family Littorinidae have been classified into four types (paucispiral types A and B, mesospiral, multispiral) and the occurrence of each reviewed by Bandel & Kadolsky (1982). Following this scheme, the opercula of *Bembicium* species are of the paucispiral type A. The coiling is most open in *B. nanum*, with an extremely acentric nucleus (Fig. 22f); no consistent differences occur in the remaining four species of the genus (Figs 14f, 17h). In *Risellopsis varia* the coiling is more tight and the nucleus more nearly central; this is the paucispiral type B (Fig. 26b). It may be noted that the genus *Peasiella*, similar in shell shape to *Bembicium*, has a multispiral operculum (Kesteven, 1903).

Bandel & Kadolsky (1982) suggested that tightly coiled opercula have evolved repeatedly amongst littorinids, from an originally paucispiral ancestral form. This was explained as an adaptation to life at high supratidal levels, where species develop a smaller and more circular aperture in order to minimise temperature stress and desiccation. Such an aperture is fitted more closely by a tightly coiled, circular operculum, and tight coiling also thickens the operculum. This suggestion is supported by *Bembicium* and *Risellopsis*, for the latter is reported to live at higher tidal levels, has a more circular aperture and a more tightly coiled operculum.

ANATOMICAL CHARACTERS

Head-foot. The appearance of the head is similar to that of other littorinids. In *Bembicium* species there is no striking colour pattern; pigmentation is a diffuse mottling on the sides of the foot, the head is darker, with fine lines of pigment across the snout and annular bands along the length of the yellowish tentacles (Fig. 2). In *Risellopsis* the head is also dark and the tentacles banded to their tips, but the front of the snout lacks pigment and there is a second white stripe across the head between the tentacles (Fig. 27e). Opercular tentacles, as seen for example in *Lacuna* and in some Eatoniellidae (Ponder, 1965, 1976) are absent.

The peculiar trochoidal shape of the shell of these two genera is reflected in the orientation of the head-foot. As expressed by Kesteven (1903), when compared with turbinatid littorinids, the animal is 'twisted half round in its shell'. Fretter (1982) viewed

this as a displacement of the anterior end of the gill over the head, which normally lies to the left. In fact the arrangement of the pallial organs is no different from that of other littorinids, if the periphery of the shell and junction of the body whorl and penultimate whorl are taken as points of reference. Rather, the head and foot have been twisted 90° to the left in relation to both shell and mantle. The explanation is probably not to be found in the compression of the

left side of the mantle cavity consequent upon the change in shell shape, as was suggested by Fretter (1982). Instead, the orientation of the animal simply allows a greater area of contact between the foot and the substrate when the animal is partly retracted and the shell lies on its base. The columellar muscle retains the same origin on the columella as is found in turbinate littorinids; it has not descended to the shell base as stated by Kesteven (1903).

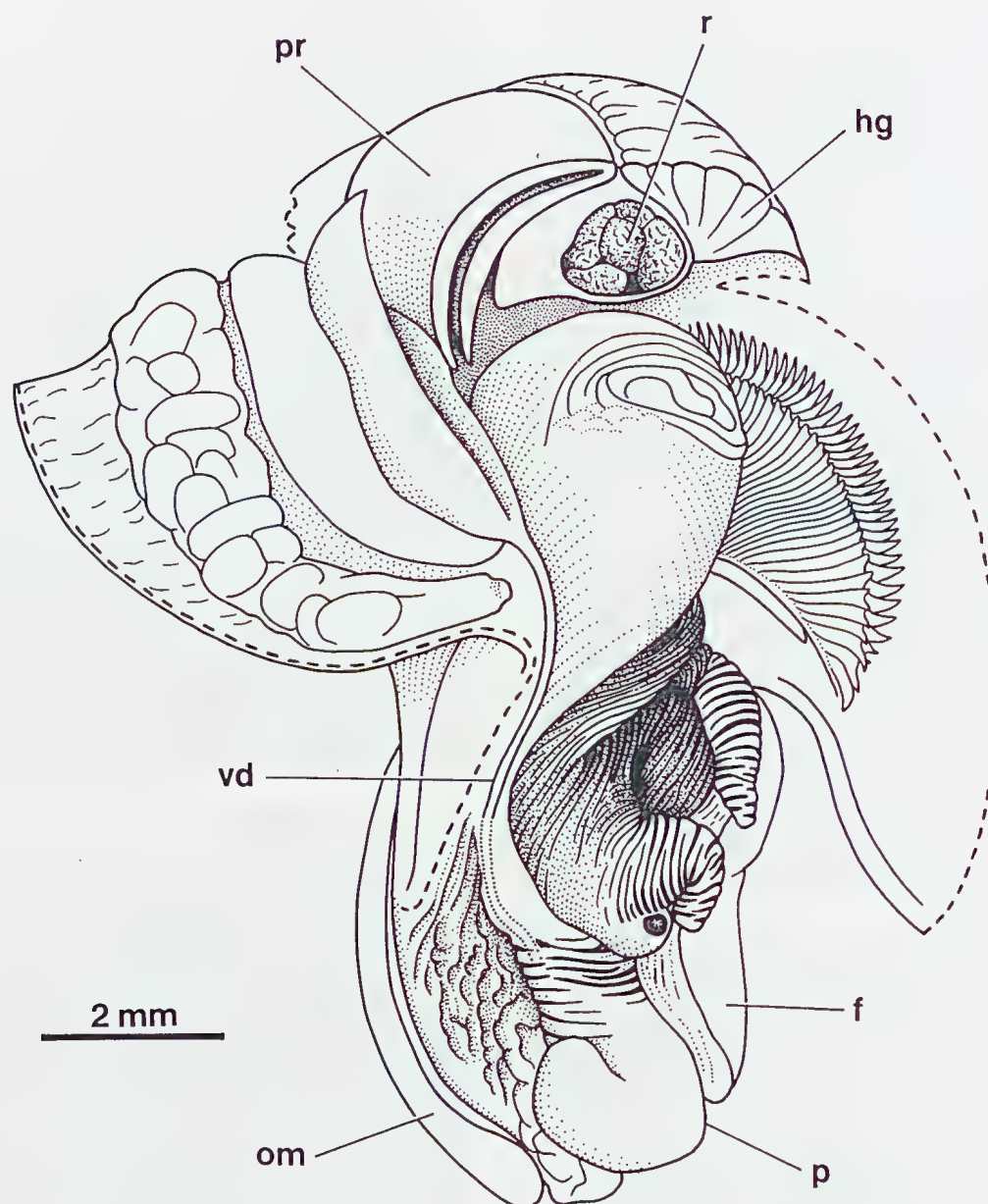


Fig.2. Male reproductive system of *Bembicium auratum* (Quoy & Gaimard), from Mallacoota, Vic. (AMS C144295). Prostate, rectum and hypobranchial gland have been sectioned, mantle cut along dotted lines and right side folded outwards. Abbreviations: f - foot; hg - hypobranchial gland; om - operculum; p - penis; pr - prostate; r - rectum; vd - anterior vas deferens.

Male reproductive tract. The plan of the male reproductive system of *Bembicium* and *Risellopsis* is typical for the family Littorinidae (Linke, 1933; Fretter & Graham, 1962; Reid, 1986). The testis overlies the digestive gland, and sperm collect in the coiled visceral vas deferens, which functions as a seminal vesicle and lies against the columella of the shell. The pallial vas deferens consists of a glandular prostate, leading to a duct or groove which carries sperm along the side of the head almost to the tip of the penis (Fig. 2). The lumen of the prostate is slit-like, open to the mantle cavity throughout its length. In *Risellopsis* the entire pallial vas deferens is an open groove, but in *Bembicium* the path of the sperm from the anterior end of the prostate, over the head and through the penis, is a closed duct. The open prostate and closed anterior vas deferens of *Bembicium* have previously been noted by Kesteven (1903), H. Anderson (1958) and Fretter (1982), while the histology of the testis, prostate and anterior vas deferens of *B. nanum* has been briefly described by Bedford (1965). The anatomy of *Risellopsis* has not previously been described.

The penis of *Bembicium* is situated just anterior to and beneath the right tentacle. When the animal is retracted into the shell, the penis is usually folded forward over the edge of the foot (Fig. 2), rather than back into the mantle cavity as in other littorinids. In general, the littorinid penis is differentiated into a wrinkled basal region, a smooth filament with abundant goblet cells (which conveys sperm into the bursa copulatrix of the female), and glandular tissue which produces an apparently adhesive mucus (Reid, 1986). In *Bembicium* the base is rather short and somewhat laterally compressed, with the ciliated sperm duct running through its ventral edge. The region corresponding to the filament is not clearly differentiated from the base except by lack of wrinkles, and in *B. vittatum* and *B. auratum* it is broader than the base and of a peculiar hammer-like or claw-like shape (Figs 12, 18). The filament is more slender in *B. melanostoma* and *B. flavescens* (Figs 8, 15a-h), and no more than a small protruberance in *B. nanum* (Fig. 15i-p). In all cases the opening of the penial sperm duct is subterminal, very markedly so in the four species with a large filamentous portion; in these the duct opens into a deep crease on the ventral surface. In *B. nanum* there is no such crease on the very small filament, but the opening is still a little behind the tip.

Although the filament of all but *B. nanum* appears to be opaque and swollen, histological sections show little differentiation between filament and base, and a lack of the subepithelial glands which are typical of other littorinids. Throughout the penis the epithelium is columnar, from 15 to 20 μm in thickness, increasing to 30 μm on the side of the base opposite to the sperm duct. The epithelial cells are possibly secretory, their bulbous distal ends staining purple in ABPAS and variously yellowish, orange or

faintly blue in Masson's trichrome. Only in *B. nanum* were goblet cells clearly visible in the epithelium, staining blue in ABPAS (indicating acidic mucins). Similar mucous cells were also scattered through the underlying connective and muscular tissue, but were not organised into glandular structures. Goblet cells are probably present in the other species also, but were poorly preserved in the specimens examined. Beneath the basement membrane of the epithelium the penis is packed with circular, longitudinal and oblique muscle fibres, with connective tissue fibres and blood spaces between. Fretter (1982) mentioned a 'semicircle of glands' in the base of the penis of *B. auratum*, but no such formation was observed in the present study.

The penis of *Risellopsis varia* is similar to that of *Bembicium* species in its position and orientation, and also in the secretory epithelium and lack of subepithelial glands. There is no clear division between the wrinkled base and smooth distal region which corresponds to the filament of other littorinids. Histologically, it can be seen that the columnar epithelium is thicker on the filament (28 to 36 μm) than on the base (8 to 19 μm), and possibly richer in goblet cells, although once again these were poorly preserved. On the edge of the base opposite to the sperm groove there is a small lobe (Fig. 27a-d), but this is not a glandular structure. The ciliated sperm groove terminates a little before the tip of the penis. At the tip a minute papilla is visible; here the epithelium is only 3 μm thick and the connective tissue layer and muscle fibres approach the surface. However, there is neither duct nor glandular tissue associated with the papilla.

Penes have not been accurately illustrated for any of the species by previous authors. Sketches were given by Kesteven (1903), Bedford (1965) and Muggeridge (1979). H. Anderson (1958) gave brief descriptions and noted that the penial shape of *B. nanum* differed from that of the other two species then recognised. Muggeridge (1979) found the proportions of the penis to be too variable for use as a taxonomic character in the genus *Bembicium*. In other littorinid groups it is now well known that the shape of the penis is a most important taxonomic character, often diagnostic of species, and this may be because penial shape is a character used for species recognition during copulation (review by Reid, 1986). In three cases penial characters can be used to separate pairs of species with almost identical shells (Sacchi & Rastelli, 1966; Murray, 1979; Reid, 1986).

In the present study the shape of the penis has been found to be a reliable character for the discrimination of the three species in the *Bembicium melanostoma* complex (*B. melanostoma* s. s., *B. vittatum*, *B. flavescens*), all with very similar shells. These species are also geographically isolated, but if penial shape is indeed a biological recognition character, the implication is that interbreeding could

not occur if their ranges were to overlap. The category of subspecies is therefore not appropriate. The similarity of penial shape is good evidence that the Queensland form of *B. auratum* is not specifically distinct from the typical form, despite recognisable differences in shell shape and colour.

It is true that penial shapes show some variation within species, as shown in the systematic accounts. This variability may be partly explained by different methods of relaxation before fixation, and possibly by differences in the state of maturity (although all specimens had mature testes). In some littorinids the penis is reduced in size or shed outside the breeding season, but in *B. auratum* and *B. nanum* Muggeridge (1979) found no change in the size of the penis once maturity was reached. Parasitism by trematodes may reduce penial size (Lysaght, 1941), but parasitised specimens were discarded in this study. Since the form of the penis is irregular, it would be difficult to quantify differences in shape. However, the differences between species are so striking that this is considered unnecessary.

The blunt form of the penis, swollen filament and absence of subepithelial glandular elements set *Bembicium* and *Risellopsis* apart from other littorinids, but do not provide any indication of relationships with other genera, at the present state of knowledge. It is not clear whether the open prostate is a plesiomorphic or apomorphic character amongst the Littorinidae. The open condition is more common, a closed prostate having been recorded only in *Cremanoconchus* (Linke, 1935) and *Littoraria* (Reid, 1986). However, amongst possible out-groups relevant to a discussion of littorinid phylogeny, the prostate is closed in *Pomatias* (Creek, 1951) and in *Lacuna* (Gallien & de Larambergue, 1938), but open in Eatoniellidae (Ponder, 1968). Similar doubt surrounds the status of the penial sperm groove. The closed condition of *Bembicium* occurs also in *Melarthaphe*, *Fossarilittorina*, *Peasiella*, some *Littoraria* species (all Reid, 1986), *Cremanoconchus* (Linke, 1935) and *Rufolacuna* (Ponder, 1976), while an open groove is found in other littorinid genera (Reid, 1986). The sperm groove is closed as a duct in *Pomatias* (Creek, 1951) and in *Lacuna* (Gallien & de Larambergue, 1938). The basal flap of *Risellopsis* is superficially similar to the penial glandular disc of the genera *Nodilittorina* and *Littoraria* (Reid, 1986), and the apical papilla is reminiscent of the mamilliform penial glands of *Littorina*, *Peasiella*, *Tectarius*, *Echininus*, *Nodilittorina* and *Mainwaringia* (Linke, 1933; Reid, 1986 and pers. obs.). Nevertheless, neither structure of *Risellopsis* is in fact glandular, and therefore they are probably not homologous with the appendages of other littorinids. An absence of penial glands, both mamilliform and disc-like, is recorded in *Cenchritis*, *Fossarilittorina*, *Melarthaphe* and rarely in *Nodilittorina*. In these cases the loss may be secondary, while in *Bembicium* it has been tentatively suggested that the absence is

plesiomorphic (Reid, 1986). No penial glands have been reported in *Pomatias* (Creek, 1951), but unspecialised subepithelial glandular cells are present in *Lacuna* (Gallien & de Larambergue, 1938; pers. obs.).

Sperm cells. In many littorinid genera the testis produces sperm of two types. In addition to the euspermatozoa (or 'typical sperm') there are rounded nurse cells, packed with yolk granules and sometimes rod-shaped inclusions (review by Reid, 1986). Nurse cells were not seen in the seminal vesicle of two living *Bembicium nanum* and four *B. auratum*, nor were they found in preserved specimens of these species or *Risellopsis varia*. However, Bedford (1965) described 'nurse cells with finely vacuolated cytoplasm and attached spermatids and spermatozoa' in the testicular tubules of *B. nanum*, and Muggeridge (1979) briefly mentioned nurse cells in *B. auratum*. It may be that nutritive cells similar to, or even homologous with, nurse cells are present during the development of euspermatozoa. Alternatively, these authors may have been mistaken, describing the artefactual agglutination of sperm which sometimes occurs in squashed preparations. Nurse cells of the type found in the seminal vesicle of other littorinids are absent in *Bembicium* and *Risellopsis*, and this may conceivably be a plesiomorphic character (Reid, 1986). It may also be mentioned that nurse cells are absent in *Lacuna pallidula* (Gallien & de Larambergue, 1938) and in *L. vineta* (pers. obs.). Further investigation of spermatogenesis is obviously required in *Bembicium* and *Risellopsis*. In *B. auratum* from Magnetic Island, Queensland, the eupyrene sperm were 220 to 240 µm in length, and 250 µm in *B. nanum* from Sydney.

Female reproductive tract. As in other littorinids, the female reproductive system consists of the ovary, overlying the digestive gland, and the oviduct, sequentially differentiated into gonadal, renal and pallial sections. The gonadal oviduct is thin walled, while the short renal portion has thick glandular walls, staining blue in MT and dark blue and purple in ABPAS. In species of *Bembicium* a short gonopericardial duct is present at the junction of the gonadal and renal sections of the oviduct. The functions of the pallial oviduct are concerned with reception and storage of sperm, fertilisation and the production of egg masses. In all littorinids the pallial oviduct is of a complex form, but the basic plan can be envisaged as a laterally flattened tube in the mantle wall, containing a dorsal groove for the passage of eggs and a ventral sperm groove. As the eggs pass anteriorly, they are first fertilised and then successively coated by albumen and other covering layers secreted by the glands of the pallial oviduct. The path of the egg groove is not straight, but is twisted into loops and spirals in a pattern characteristic for each genus in the family (see diagrammatic Fig. 6 in Reid, 1986). At the anterior

end, a ventral bursa receives sperm at copulation, and the ventral sperm groove leads posteriorly to the seminal receptacle, where sperm are stored. The structure of the pallial oviduct in the Littorinidae has recently been reviewed by Reid (1986). From the anterior opening of the pallial oviduct into the mantle cavity, a ciliated tract runs anteriorly to the ovipositor, an unpigmented raised area with a medial groove, on the right side of the head below the eye.

When a mature female *Bembicium* is removed from the shell, the pallial oviduct is conspicuously visible, occupying half a revolution on the uppermost surface of the animal (Fig. 3a). The dark red hypobranchial gland is closely applied to the mediodorsal side of the pallial oviduct, lying mostly below the peripheral keel of the shell, and the rectum lies against the medial surface. Most of the anterior and medial parts of the pallial oviduct are taken up by the greatly enlarged jelly gland, opaque whitish, cream or fawn in fresh and preserved material, and often with the internal septation visible externally. The posterolateral part of the pallial oviduct is comprised of the albumen gland, the anterior part of which is opaque cream or brown (the opaque albumen gland) while the posterior region is usually paler and more translucent (the translucent albumen gland). The spiral form of the albumen gland is clearly visible without dissection, but of the several previous authors who have described the reproductive system of *Bembicium*, only Kesteven (1903) has noted this feature. Careful dissection and serial sectioning are required to trace the ducts on the ventral side of the oviduct (Fig. 4).

The opening into the mantle cavity is about one quarter of the length of the pallial oviduct behind the anterior limit of the jelly gland (Fig. 4c), and lies on the medial side of a swollen chamber surrounded by a muscle layer up to 120 μm in thickness. The aperture is a small and inconspicuous slit (approximately 0.3 mm long) in all the specimens of *Bembicium* examined, and contrary to the observations of Fretter (1982), does not resemble the large slit-like opening seen in *Pomatias* (Creek, 1951), although it is possible that the aperture may be enlarged during oviposition. The large, muscular bursa copulatrix (muscle layer 60 to 170 μm thick) separates from the ventrolateral side of the anterior chamber of the oviduct almost adjacent to the aperture (Fig. 4, section 3). Sperm in the bursa were found to be orientated and attached to the epithelial lining, in contrast to the observation of Bedford (1965). Almost simultaneously, a narrow and inconspicuous duct 70 μm in diameter separates from the anterior chamber and runs posteriorly to the crescent-shaped seminal receptacle, which lies far back, adjacent to the renal oviduct and posterior to the bursa (Fig. 4a,c). An equally long duct, running parallel and dorsal to that to the seminal receptacle, carries the ova forwards from the renal oviduct to the anterior

chamber, where fertilisation probably occurs. This extension of the renal oviduct has a diameter of 150 to 300 μm (including a muscle coat four fibres in thickness), with a ciliated columnar epithelium staining blue in MT and magenta in ABPAS. It is distinguished from the true renal oviduct by its thinner, non-glandular walls and by its staining reactions, and is probably of pallial origin. Neither of the two previous detailed accounts of the reproductive system of *Bembicium* (H. Anderson, 1958; Bedford, 1965) have described this unusual feature of the anterior position of the meeting point of ova and sperm.

From the anterior chamber, fertilised ova pass posteriorly into the morphologically dorsal egg groove. This is initially surrounded by the opaque albumen gland, staining pale blue in MT and purple to blue in ABPAS (indicating mixed and acidic mucins). Posteriorly, the egg groove is twisted into a doubly wound spiral, of two and one half revolutions, the greater part of which is surrounded by the translucent albumen gland, staining colourless in MT and red to magenta (neutral mucins) in ABPAS. The final half revolution of the egg groove, and the straight section anterior to the spiral portion, run through the large jelly gland. The walls of the jelly gland are thrown into folds, to form incomplete septa across the long axis of the pallial oviduct. Anteriorly, the jelly gland is divided into inner and outer chambers (Fig. 4, section 2); the inner chamber (closest to the rectum) ends blindly posteriorly, but the two chambers communicate anteriorly. In MT the jelly gland stains colourless to pale blue, and in ABPAS mostly magenta (neutral mucins), but sometimes with purple or bluish areas. Since the glandular part of the pallial oviduct is a laterally flattened tube twisted into a spiral on the dorsal side only, the albumen and jelly glands have a common lumen, with interconnection in the axis of the spiral, as shown in the serial sections (Fig. 4, sections 6 and 7). Both albumen and jelly glands have a similar histological structure, consisting of very tall (80 to 360 μm), columnar cells with ciliated supporting cells in a glandular epithelium (Bedford, 1965). Throughout the pallial oviduct, but especially in the jelly gland, there are scattered, flask-shaped cells in the epithelia which contain granules staining red in MT and magenta in ABPAS. These have also been noted by Bedford (1965), and may be excretory amoebocytes (Linke, 1933).

The histology of the female reproductive system of *Bembicium nanum* has been described in detail by Bedford (1965). Some differences in terminology should be noted: the term 'renal oviduct' should be restricted to the short, thick-walled, swollen region between the gonadal and pallial sections; the 'vagina' is the muscular chamber opening to the mantle cavity. Both H. Anderson (1958) and Kesteven (1903) referred to the entire pallial oviduct as the 'uterus'. Contrary to the descriptions of H.

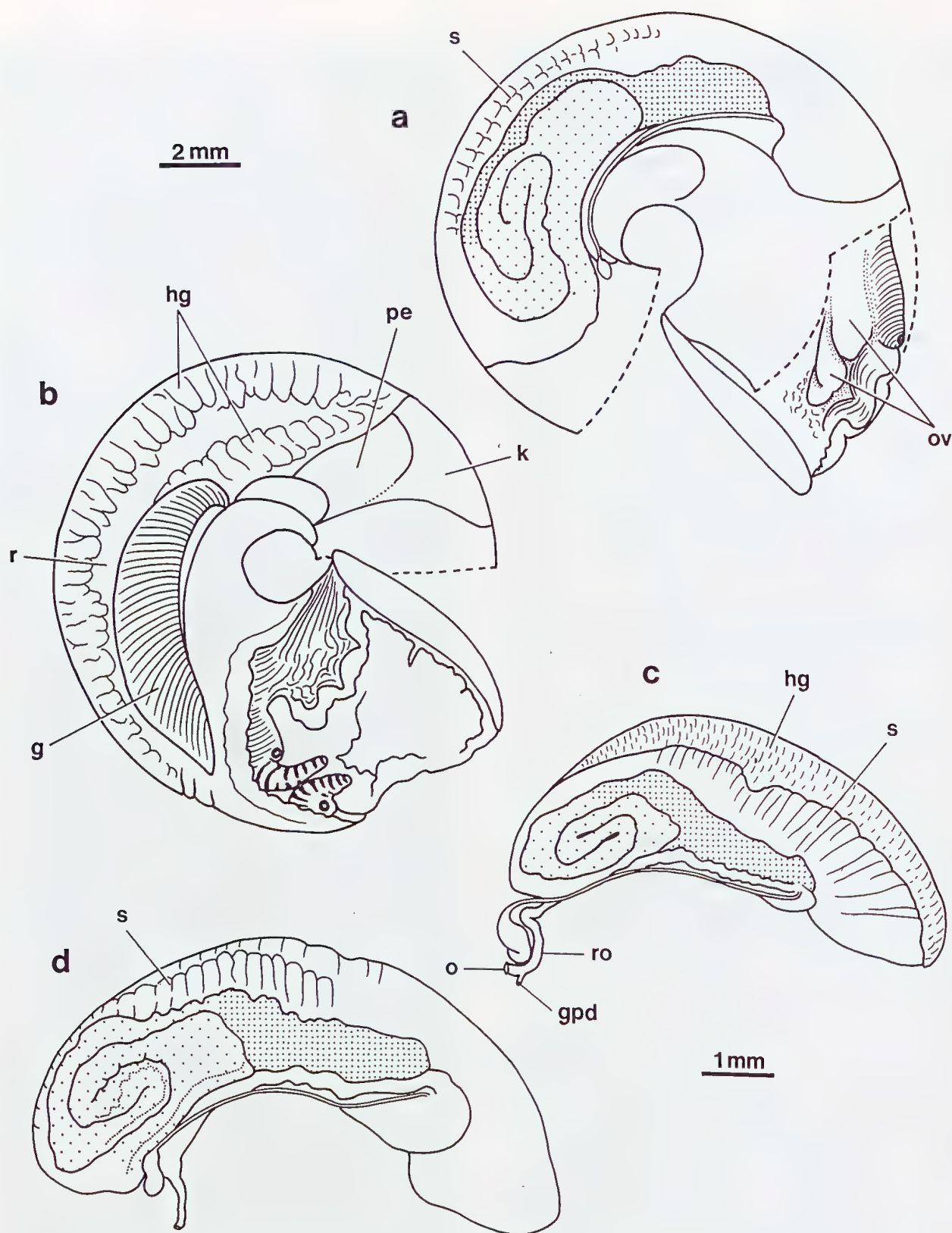


Fig. 3. a, b *Bembicium melanostoma* (Gmelin), from Pittwater, Tas. (AMS C144402), female removed from shell; a, viewed from apex of shell, with part of mantle cut away to show ovipositor; b, viewed from base of shell; c, pallial oviduct of *Bembicium nanum* (Lamarck), from Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); d, pallial oviduct of *Bembicium auratum* (Quoy & Gaimard), from North Keppel Island, Qld. (AMS C144367). Abbreviations: g - gill; gpd - gonopericardial duct; hg - hypobranchial gland; k - kidney; o - ovarian oviduct; ov - ovipositor; pe - pericardium; r - rectum; ro - renal oviduct; s - septa of jelly gland; dark stipple, opaque albumen gland; light stipple, translucent albumen gland.

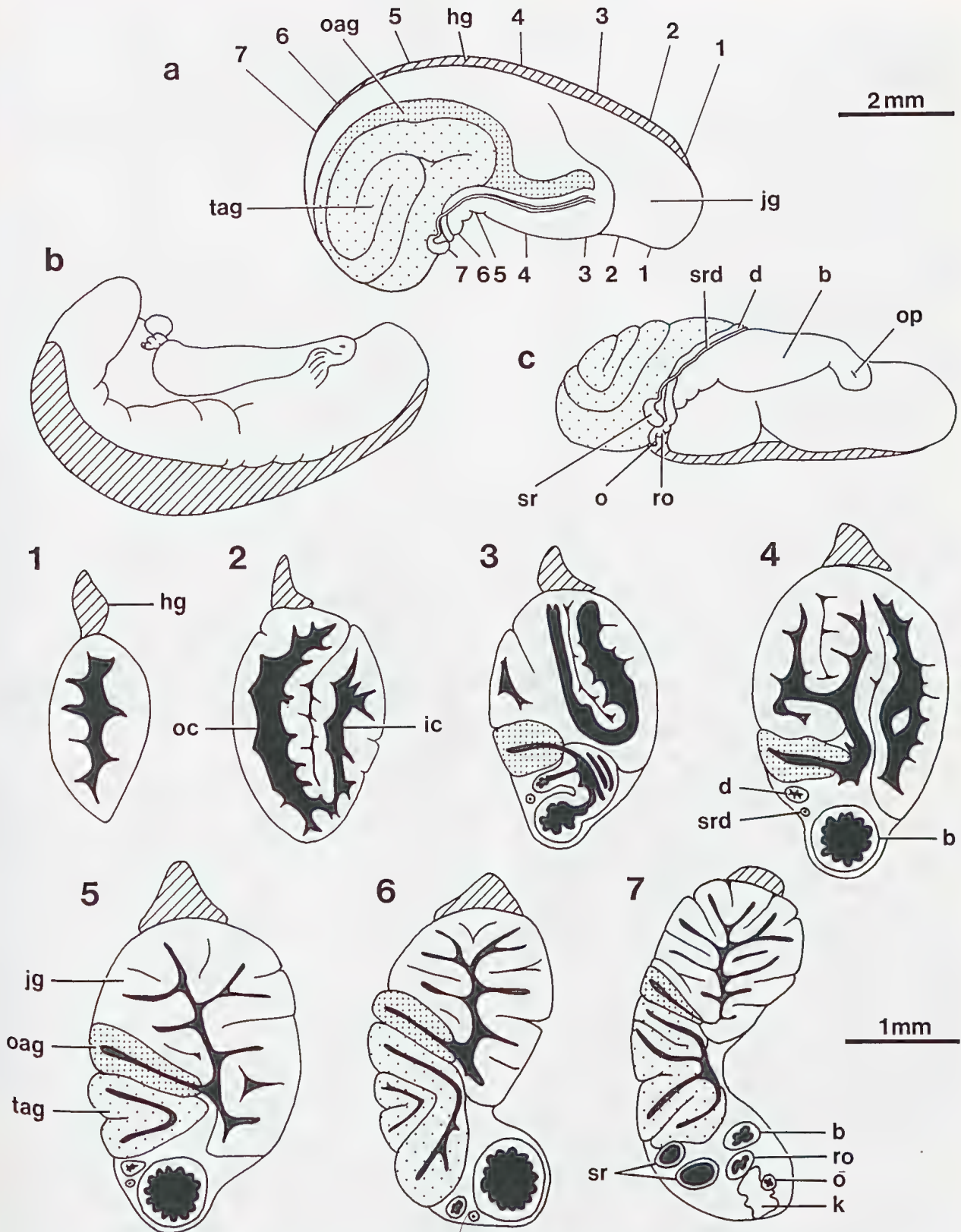


Fig.4. Pallial oviduct of *Bembicium auratum* (Quoy & Gaimard), from Magnetic Island, Qld (BMNH): a, lateral view; b, medial view; c, ventral view; 1-7, serial sections. Abbreviations: b - bursa; d - duct from renal oviduct to pallial oviduct; hg - hypobranchial gland (cross hatched); ic - inner chamber of jelly gland; jg - jelly gland; k - part of kidney; o - ovarian oviduct; oag - opaque albumen gland (dark stipple); oc - outer chamber of jelly gland; op - opening of muscular chamber of pallial oviduct into mantle cavity; ro - renal oviduct; sr - seminal receptacle; srd - duct to seminal receptacle; tag - translucent albumen gland (light stipple).

Anderson (1958) and Bedford (1965) there is no ventral sperm groove or channel in the lumen of the pallial oviduct, because sperm and ova meet anteriorly, in the muscular chamber.

No significant differences in the form of the pallial oviduct were observed amongst the five species of *Bembicium*. The appearance of the oviducal glands showed some variation with the degree of hydration of the tissue, being swollen and translucent in formalin, shrunken and opaque in 70% ethanol. Kesteven (1903) noted a reduction in the size of the reproductive system of *B. nanum* outside the breeding season, although Bedford (1965) found no change throughout the year.

The female reproductive system of *Risellopsis varia* is similar to that in the genus *Bembicium*. Externally, the pallial oviduct can be seen to consist of a swollen jelly gland and a posterior spiral albumen gland of two and one half revolutions (Fig. 5). There are, however, some notable differences. The renal oviduct runs directly into the opaque albumen gland (Fig. 5c), and the latter is contained entirely within the spiral portion of the pallial oviduct (Fig. 5a). Nevertheless, the duct of the seminal receptacle joins the oviduct in an anterior position, as in *Bembicium*. Presumably, sperm reach the unfertilised ova by means of the sperm groove, which is a ciliated ventral channel (Fig. 5, section 3) continuous with the lumen of the jelly gland, so that fertilisation can occur as the ova enter the opaque albumen gland from the renal oviduct. The duct to the seminal receptacle, and also the ventral channel and jelly gland, separate from the muscular anterior chamber anterior to the small opening of the pallial oviduct into the mantle cavity (Fig. 5, sections 1 and 2). As in *Bembicium* species, the jelly gland is divided into two chambers in the straight part of the pallial oviduct (Fig. 5, section 3), and these communicate anteriorly, while the inner chamber ends blindly posteriorly. In the single serially sectioned specimen of *R. varia* three regions of the jelly gland could be distinguished by their staining reactions using the ABPAS technique. The inner chamber stained dark magenta and purple, the outer chamber and its continuation into the spiral portion adjacent to the hypobranchial gland stained purple and blue, and the bulk of the jelly gland medial to the spiral albumen gland stained pale magenta. It may be noted that in unstained preserved specimens of *Bembicium* the part of the jelly gland corresponding to the outer chamber frequently appears more white and opaque than the rest, implying some differentiation within the gland, although this was not evident in the serial sections. As in *Bembicium*, the albumen gland of *R. varia* is differentiated into opaque and translucent parts. The spiral form of the pallial oviduct is rather more clear externally in *R. varia* than in *Bembicium* species, for in the former the ciliated grooves of the albumen gland and ventral channel contain black pigment.

The overall similarity of the pallial oviducts of *Bembicium* and *Risellopsis* confirms the close relationship between these genera, while comparison with other members of the family shows important differences. The anterior position of the opening of the duct to the seminal receptacle is not found in any other littorinids and is a possible synapomorphy of the two genera. Out-group comparison is a problem, because a seminal receptacle is absent in *Pomatias* (Creek, 1951) and *Lacuna* (Gallien & de Larambergue, 1938) and the homology of the posterior sperm sac of Eatoniellidae (Ponder, 1968) is uncertain. However, in the Rissoacea the seminal receptacle and its junction with the pallial oviduct are in a posterior position (e.g. Ponder, 1983, 1985). Assuming that the posterior position for the junction of renal oviduct and albumen gland, and of the duct to the seminal receptacle (as found in all other littorinids), are primitive, then *Risellopsis* represents an intermediate stage in the evolution of the condition seen in *Bembicium*. In *Risellopsis* the duct of the seminal receptacle has lengthened and its opening to the pallial oviduct has migrated anteriorly. This long duct was probably not achieved by closure of the sperm groove to form a duct, since both structures are present in *Risellopsis*. In this intermediate stage the route of the sperm would seem to be unnecessarily lengthened. Shortening of the route was achieved by bringing the junction of the renal oviduct with the albumen gland (the site of fertilisation) forwards. In the process the ventral sperm groove was eliminated, fertilised ova being passed directly into the anterior prolongation of the albumen gland.

The partial division of the jelly gland into two chambers is another unusual feature of *Bembicium* and *Risellopsis*, which may be synapomorphic. No such division is found in species of *Littorina* with enlarged jelly glands which produce a benthic gelatinous spawn (Linke, 1933; Hannaford Ellis, 1979; Fretter, 1980). Amongst possible out-groups, a similar arrangement occurs only in *Lacuna* (pers. obs.).

Histologically, the jelly glands of *Bembicium* and *Risellopsis* are similar to that described in *Littorina obtusata* (L.) by Linke (1933), consisting of a glandular epithelium of very tall columnar cells. However, in the other littorinid genera so far examined (including *Littorina*, Linke, 1933; Hannaford Ellis, 1979; *Littoraria*, Reid, 1986; *Peasiella*, *Nodilittorina*, *Mainwaringia*, all pers. obs.), the albumen and capsule glands are subepithelial, and the passage of the egg groove through them is lined by a non-secretory ciliated epithelium. In contrast, the albumen glands of *Bembicium* and *Risellopsis* are epithelial, of the same structure as the jelly gland. Despite this difference from the other littorinid genera listed above, the same differentiation of the albumen gland into opaque and translucent parts is seen in both groups.

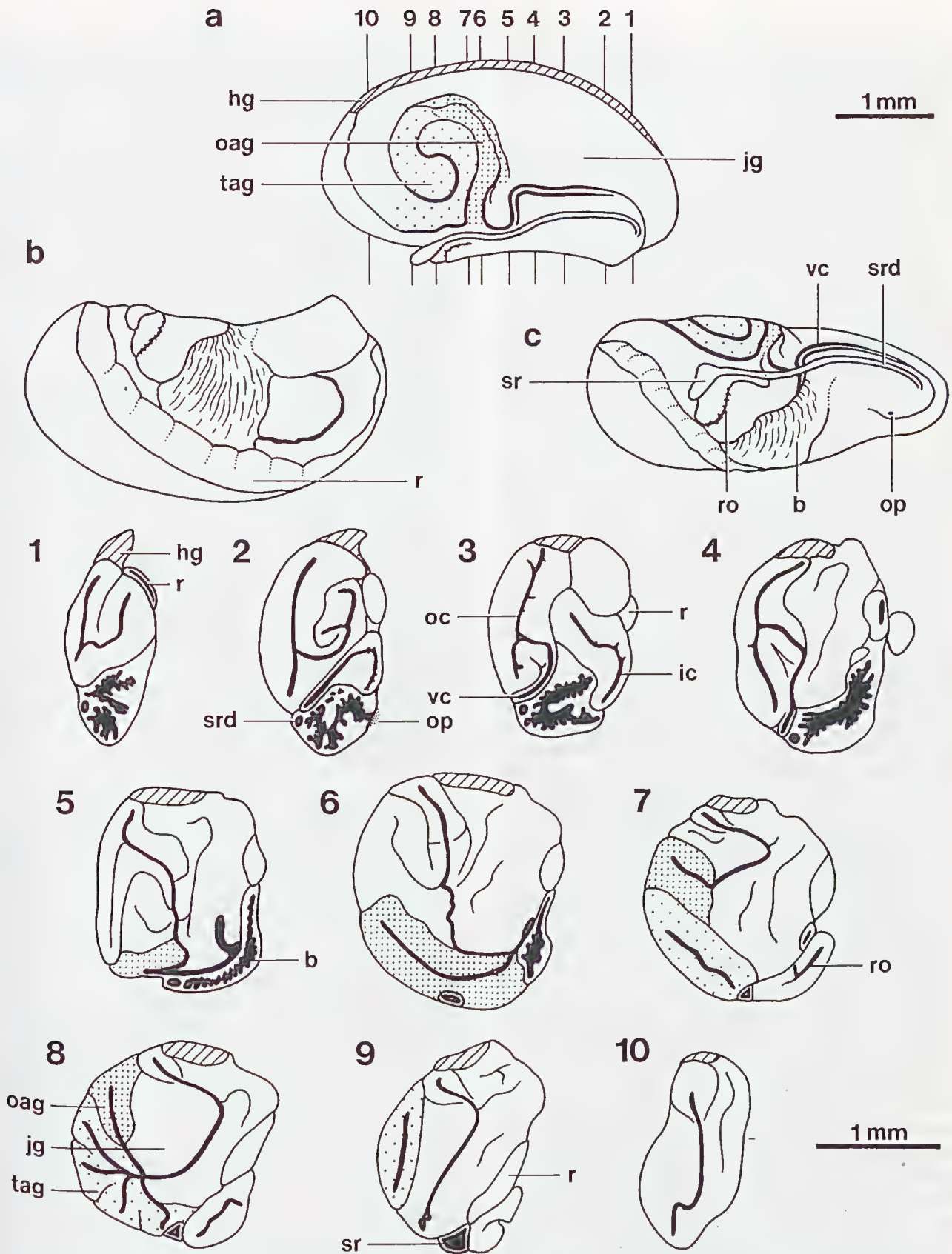


Fig.5. Pallial oviduct of *Risellopsis varia* (Hutton), from Ringaringa, Stewart Island, New Zealand (NMNZ 80806): a, lateral view; b, medial view; c, ventral view; 1-10, serial sections. Abbreviations: b - bursa; hg - hypobranchial gland (cross hatched); ic - inner chamber of jelly gland; jg - jelly gland; oag - opaque albumen gland (dark stipple); oc - outer chamber of jelly gland; op - opening of muscular chamber of pallial oviduct into mantle cavity; r - rectum; ro - renal oviduct; sr - seminal receptacle; srd - duct to seminal receptacle; tag - translucent albumen gland (light stipple); vc - ciliated ventral channel.

In all the possible out-groups, *Pomatias* (Creek, 1951), Eatoniellidae (Ponder, 1968) and *Lacuna* (pers. obs.) the glands of the pallial oviduct are epithelial, so this feature is likely to be plesiomorphic in *Bembicium* and *Risellopsis*.

The absence of capsule glands in *Bembicium* and *Risellopsis* is also noteworthy. Their distribution in other littorinids suggests that these glands produce the egg capsule and the jelly within it (Reid, 1986). The types of spawn in Littorinidae and their evolution are discussed in the following section. Here it may be pointed out that in *Littorina* species producing benthic gelatinous spawn an opaque capsule gland is present, although of small size (Hannaford Ellis, 1979; Fretter, 1980; Reid, 1986), suggesting that they have been derived from ancestors which produced pelagic capsules. In *Lacuna*, also producing a benthic gelatinous spawn, capsule glands are absent (pers. obs.). Taking *Lacuna* as an out-group, it is tentatively suggested that the absence of capsule glands in *Bembicium* and *Risellopsis* is plesiomorphic. It will be necessary to examine the oviducts of other littorinids with gelatinous spawn to test this hypothesis. The homologies of the so-called 'capsule gland' of *Pomatias* (Creek, 1951) and of the oviducal glands of Eatoniellidae (Ponder, 1968) are doubtful.

The suggestion that *Bembicium* species may be hermaphroditic was first made by Tenison-Woods (1877), although it is likely that he confused the prominent ovipositor of females with the penis of males (Kesteven, 1903). Abnormalities do occur, however. Muggeridge (1979) found some females of both *B. auratum* and *B. nanum* with vestigial penes, which she suggested may have been induced by alteration of the hormonal balance following recovery from parasitic infection (see Streiff & Le Breton, 1970). In the present study a single unparasitised male *B. auratum* was collected at North Harbour, Sydney, with a normal penis and prostate, but with a mixed gonad containing both eggs and sperm. True protandrous hermaphroditism has been found amongst the Littorinidae only in the genus *Mainwaringia* (Reid, in prep.).

Egg masses. The eggs of *Bembicium* are deposited in small ovoid or irregular gelatinous masses, attached in closely packed clusters to a hard substrate. The egg masses have been described in detail in three species. In *B. auratum* the individual gelatinous masses are bean-shaped, 2 to 3 by 1 to 1.5 mm, and each contains 60 to 100 eggs; these are deposited over an area of 3 to 5 cm² on the undersides of stones in rock pools, making a total of up to 12,500 eggs. Individual eggs range in diameter from 115 to 122 µm, and are each surrounded by albumen in a transparent, ovoid, egg envelope, measuring 215 to 234 by 240 to 272 µm (H. Anderson, 1958; D.T. Anderson, 1962; Muggeridge, 1979). The egg masses of *B. nanum* are oval, containing 100 to 200 creamy white eggs 100 µm in diameter, and each surrounded

by an ovoid, transparent envelope 200 to 220 by 190 to 210 µm; the spawn is attached to the rock in fissures or under weed, in the adult habitat (D.T. Anderson, 1961). Both these species hatch as veligers after ten to 12 days (D.T. Anderson, 1961, 1962).

The eggs of *B. vittatum* are larger, of an average diameter of 172 µm, contained in envelopes 404 by 460 µm, and are deposited in irregularly shaped masses each containing eight to 30 eggs (H. Anderson, 1958, as *B. melanostoma*). The larger eggs and greater supply of albumen is related to the probable lecithotrophic development of this species, which lacks a planktonic veliger stage (H. Anderson, 1958).

Pilkington (1974) has described the egg masses of *Risellopsis varia*. These are irregular in shape, each 5 to 6 mm in diameter, flat at first but becoming convex with development. Veligers hatch after 12 days in the laboratory. In a sample of egg masses preserved in alcohol from Stewart Island (NMNZ M80806, pers. obs.), the individual masses measured 2 to 3 mm in diameter and were closely attached to the rock and each other in clusters of 20 or more. Individual masses contained 250 to 500 eggs, measuring 103 to 119 µm in diameter, and enclosed in ovoid envelopes 122 to 178 by 144 to 189 µm.

Amongst other littorinids, production of benthic gelatinous spawn is relatively unusual, having been recorded in six species of *Littorina* (Kojima, 1958; Buckland-Nicks *et al.*, 1973; Fretter, 1980), two of *Laevilittorina* (Picken, 1979; Simpson & Harrington, 1985), two of *Laevilacunaria* (Picken, 1979), two of *Pellilittorina* (Picken, 1979) and one of *Macquariella* (Simpson and Harrington, 1985). This type of spawn is also known in at least two species of *Lacuna* (Thorson, 1946). In all these cases, except *Lacuna vincta* (as *L. divaricata* in Thorson, 1946), the planktonic stage is eliminated, and juveniles hatch directly from the egg mass. Amongst littorinids, the combination of benthic spawn and a planktonic veliger stage is known only in *Bembicium nanum*, *B. auratum*, *Risellopsis varia* and *Lacuna vincta*.

It has been suggested that a benthic gelatinous spawn is primitive in the Littorinidae and in *Lacuna* (Fretter, 1980). However, Reid (1986) argued that at least in *Littorina* the benthic spawn was derived from an ancestral state with pelagic capsules. In view of the absence of capsule glands in *Bembicium*, *Risellopsis* and *Lacuna*, as discussed above, the conflicting hypotheses could be resolved by the suggestion that a benthic spawn is plesiomorphic in these three genera, and secondarily derived in *Littorina*. All the littorinids with benthic spawn have in common a mainly cool temperate, arctic or antarctic distribution (although *B. auratum* extends to northern Queensland), conforming to a general tendency towards reduction or elimination of planktotrophic development in benthic marine animals inhabiting high latitudes (Thorson, 1950; Jablonski & Lutz, 1983). If viewed as an ecological

adaptation, it is possible that benthic egg masses may have appeared independently in several clades. Further information, especially on the anatomy and relationships of the four antarctic genera with benthic spawn listed above, will be required to resolve this problem.

Radula. The radulae of *Bembicium* and *Risellopsis* are of the normal taenioglossate type, with seven teeth in each row, a central rachidian tooth flanked by a lateral and an inner and an outer marginal on each side. In *Bembicium* the length of the central tooth is approximately 1.6 times its width, when the flat radula is viewed from above (e.g. Fig. 19). The central tooth bears one large anterior cusp, flanked by two smaller cusps which may be reduced to mere denticles. The thickened shaft of the central tooth is supported by lateral 'wings', and the posterior edge of the base is rounded or truncated, without projections. Each of the paired teeth in a row also bears one major cusp, closely similar in size and shape to that of the central tooth. In addition each lateral tooth bears one to two (rarely three) small inner cusps and one small outer cusp. The base of the lateral is broad, hollowed out into a deep groove in which lies the shaft of the inner marginal. The cusp pattern of the inner marginal is similar to that of the lateral, with two small inner cusps and one small outer cusp flanking the main cusp. The outer marginals bear only one to three small inner cusps, in addition to the main cusp, which is itself smaller than those of the outer teeth. Few figures of the radula of *Bembicium* have previously been published, all poorly drawn (Troschel, 1856–63; Gray, 1857; Woodward, 1866; Kesteven, 1903).

The radula of *Risellopsis* is basically similar to that of *Bembicium* (Fig. 26c,d; Hutton, 1882; Kesteven, 1902). The cusps of the rachidian tooth are relatively reduced in size, but an additional pair of denticles is present, the thickened shaft is narrowed, and the posterior edge of the base elaborated to give three rounded projections. The major cusps of the lateral and inner marginal teeth are not pointed or leaf-shaped as in *Bembicium*, but bluntly truncated. Cusp numbers and relative sizes on the paired teeth are similar to *Bembicium*; the lateral bears two to three small inner cusps, a major cusp and one to two small outer cusps; the inner marginal bears two small inner cusps, a major cusp and a small outer cusp; the outer marginal bears two inner cusps and a major cusp.

The radula of both genera fall within the morphological range of other members of the Littorinidae (e.g. Rosewater, 1970, 1972, 1980; Bandel, 1974; Ponder, 1976; Arnaud & Bandel, 1978; Bandel & Kadolsky, 1982). In particular the deep gutter or 'littorinid embayment' of the lateral tooth is characteristic of the family (Troschel, 1856–63; Rosewater, 1980; Bandel & Kadolsky, 1982). In comparison with other littorinids, the radula is of a rather unspecialised type, corresponding to the 'moderate' type of Rosewater (1980) and the group

exemplified by *Littorina littorea* of Bandel (1974). This type may not be primitive for the family as a whole; the ancestral condition may be represented by the type with a broad central tooth with at least five cusps, as found in the Eatoniellidae (Ponder & Yoo, 1978), in Lacuna (Troschel, 1856–63), and in some antarctic littorinids (Ponder, 1976; Arnaud & Bandel, 1978). Nevertheless, the radulae of *Bembicium* and *Risellopsis* clearly lack the extreme specialisations found in *Echininus* and some *Nodilittorina* species (Bandel & Kadolsky, 1982).

A striking feature of the radula of *Bembicium* is the lack of differentiation between teeth in a row, and the similarity of their cusp shapes. This similarity may be under developmental constraint; the form of the major cusps shows considerable variation within *Bembicium* species, but the cusps of all teeth in a row vary together in the same way (Fig. 19). Again in contrast to many other littorinids, the cusps of the teeth are not recurved posteriorly, but instead are deflected anteriorly, so that the angle between the cusp and the shaft of each tooth is 110° to 140° . The small number of cusps on the outer marginal teeth is also unusual in the family (Bandel, 1974).

Radular characters have been used to discriminate between species of littorinids (e.g. Bandel, 1974; Bandel & Kadolsky, 1982), but this practice has not been adequately validated by studies of intraspecific variability. Where intraspecific variation has been considered, it has been found to be rather high (Borkowski, 1975; Goodwin & Fish, 1977). In the Littorinidae, radular characters appear to be taxonomically useful only at the generic and subgeneric levels in most instances (Reid, 1986). In this study of *Bembicium*, ten specimens of *B. auratum* were examined, and showed an exceptionally high degree of variability in cusp shape within this species (Fig. 19). Variation was not a consequence of differences in orientation of the specimen or angle of the cusps. All radulae were taken from large adults, and there was no correlation with sex. Variation within a sample from a single locality was as great as that between widely separated localities, and no geographical trend was evident. A similar degree of variation was found in the four other species of the genus, although only five radulae of each were examined. This variability precluded the use of radular characters as taxonomic criteria in *Bembicium*. Four specimens of *Risellopsis varia* showed close similarity of cusp form.

Alimentary system, pallial complex and nervous system. The alimentary system of *Bembicium* and *Risellopsis* is similar to that of other littorinids (illustrated by Fretter & Graham, 1962; Reid, 1986). A pair of pale, thin-walled oesophageal pouches arise from the ventral side of the anterior oesophagus just posterior to the buccal mass; these pouches are not bi-lobed as in *Littoraria* (Reid, 1986). The mid-oesophagus is glandular and cream in colour, with the coiled radular sac closely attached to its upper

surface. One important, and probably apomorphic, feature of both genera is the position of the salivary glands, which lie entirely anterior to the nerve ring around the oesophagus (Fig. 6a). They are pinkish

red in colour, often fused together in the midline, and of large size (one to four times as large as the oesophageal pouches). Because of their large size, the salivary glands appear in a rather posterior position,

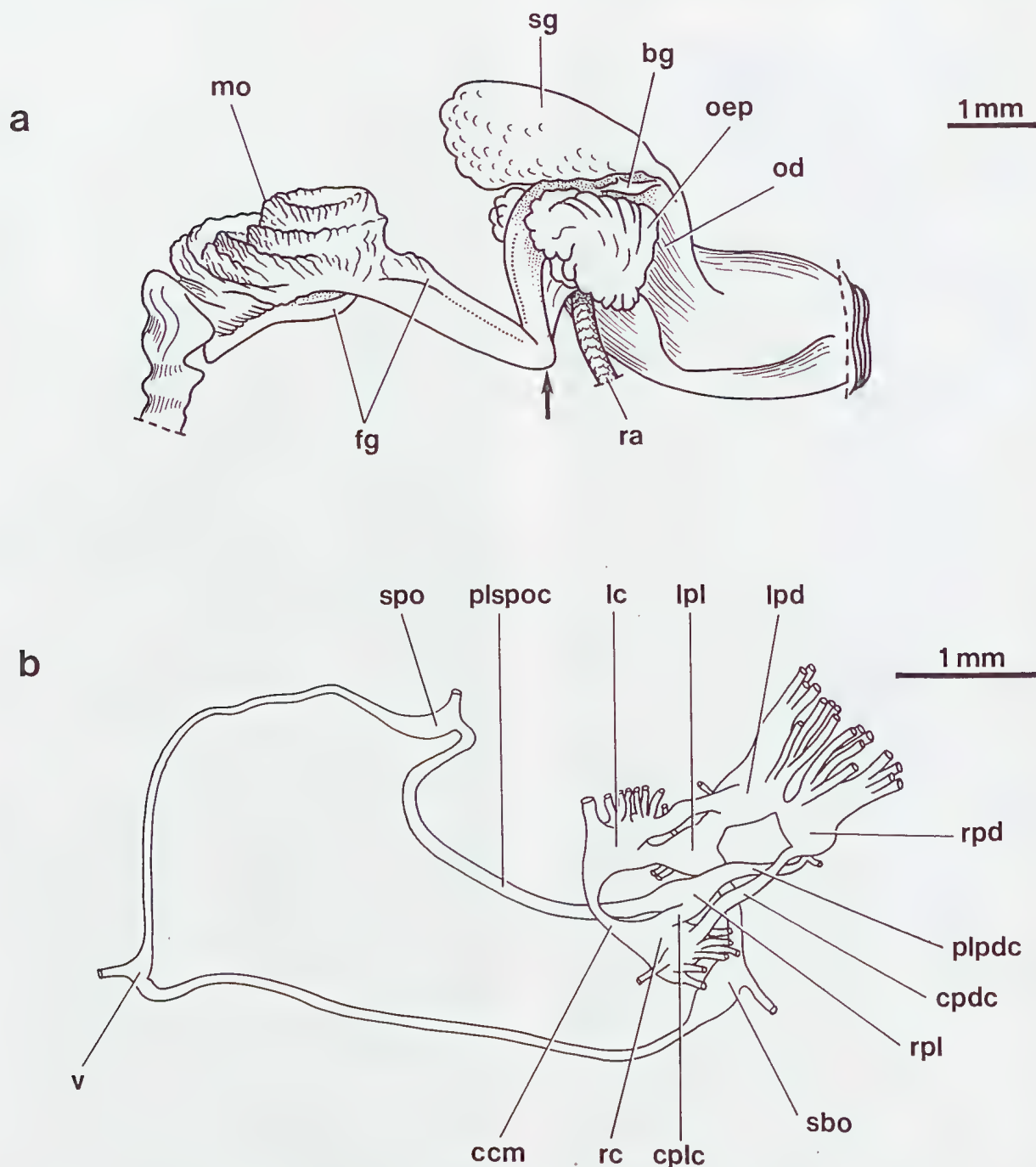


Fig. 6. *Bembicium auratum* (Quoy & Gaimard), from Nelson's Bay, Port Stephens, N.S.W. (AMS C144288): a, foregut, with coil of radular sac removed from its position overlying mid-oesophagus (on which it has left an impression, an artefact of preservation); b, principal ganglia of nervous system. Abbreviations: bg - buccal ganglion; ccm - cerebral commissure; cpdc - cerebropedal connective; cplc - cerebropleural connective; fg - good groove; lc - left cerebral ganglion; lpd - left pedal ganglion; lpl - left pleural ganglion; mo - mid-oesophagus with imprint of radular sac; od - position of odontophore; oep - oesophageal pouch; plpdc - pleuropedal connective; plspoc - pleurosupraoesophageal connective; ra - radula; rc - right cerebral ganglion; rpd - right pedal ganglion; rpl - right pleural ganglion; sbo - suboesophageal ganglion; sg - salivary gland; spo - supraoesophageal ganglion; v - visceral ganglion; arrow marks position of nerve ring around oesophagus.

partly overlying the radular sac, but neither ducts nor glandular material pass through the nerve ring. A narrow posterior extension of the glands, apparently along a blood vessel, is sometimes present, but terminates in front of the nerve ring. Amongst other littorinaceans, the salivary ducts pass through the nerve ring to posterior glands in *Littorina* (Fretter & Graham, 1962), *Nodilittorina* and *Cenchritis* (pers. obs.), either ducts or glands pass through in *Macquariella*, *Laevilittorina* and the *Eatoniellidae* (Ponder, 1983), and the glands are constricted into two parts by the nerve ring in *Littoraria* (Reid, 1986) and in *Lacuna* (pers. obs.). The salivary glands pass through the nerve ring in the majority of mesogastropods, and this state is presumably primitive (Ponder, 1983). The stomach of *Bembicium* is like that of other littorinids, although the U-shaped proximal region is shortened, and there is only a single opening of the ducts from the digestive gland, rather than three as in *Littorina* (Fretter & Graham, 1962) and *Littoraria* (Reid, 1986).

Of the structures of the pallial complex, the hypobranchial gland is particularly well developed in *Bembicium* and *Risellopsis*. It is dark red in colour, and may reach a width of 2.0 mm in large specimens of *B. auratum* and *B. nanum*.

The nervous system of *B. nanum* has been illustrated by Kesteven (1903, as *Risella melanostoma*), and that of *B. auratum* is shown in Fig. 6b. The arrangement is similar to that of *Littorina* (Bouvier, 1887; Fretter & Graham, 1962), although relative to the size of the ganglia, the connectives and commissures forming the ring around the oesophagus are condensed. As a measure of the degree of condensation of the supraoesophageal nerve tract, Davis *et al.* (1976) have defined the RPG ratio (length of the pleuro-supraoesophageal connective divided by the sum of the lengths of the supraoesophageal ganglion, pleuro-supraoesophageal connective and right pleural ganglion). The lengths of ganglia are difficult to measure precisely in *Bembicium*, but an RPG ratio for *B. auratum* (Fig. 6b) was approximately 0.76 and for *B. nanum* (from figure by Kesteven, 1903) 0.69, which are similar to the figures 0.72 and 0.84 measured by Davis *et al.* (1976) from published figures of *Littorina littorea*.

BIOLOGY AND ECOLOGY

Habitat, predation and competition. Since species of *Bembicium* are common in the littoral zone, there is a considerable amount of information available about various aspects of their ecology. Their occurrence is frequently mentioned in general accounts of intertidal zonation. *Bembicium melanostoma* is found in the eulittoral, or barnacle, zone on sheltered rocky shores and in lagoons (Guiler, 1952a,b) and also, in Victoria, amongst

mangroves (Macpherson & Gabriel, 1962). In an enclosed lagoon in southern Tasmania, Guiler (1951) recorded the species in a salt marsh, and found densities of up to 86/m² on sandy mud between the marsh and the *Zostera* belt. The closely related species *B. vittatum* occupies a similar range of habitats in South Australia (Womersley, 1956; H. Anderson, 1958; Womersley & Edmonds, 1958; all as *B. melanostoma*) and in Western Australia, where a density of 1.82/m² (biomass 1.26 g/m²) was recorded on sandflats in Oyster Harbour (Wells & Threlfall, 1980, as *B. auratum*). The third member of the *melanostoma* group, *B. flavescens*, has been reported from stones on flat muddy beaches on Lord Howe Island (Etheridge, 1889), and from the upper littoral on exposed rock platforms (museum records, AMS).

Throughout its wide geographical range, *B. auratum* occurs on the roots and trunks of mangroves, in estuaries and in sheltered rocky bays, and is only rarely found on rocky or coral substrates on the open coast (Stephenson *et al.*, 1931, as *B. melanostoma*; H. Anderson, 1958; Chalmer *et al.*, 1976; Roberts & Wells, 1980, both as *B. melanostomum* (sic); Branch & Branch, 1980). This species may be one of the dominant molluscs in mangroves and at the mouths of estuaries (Roberts & Wells, 1980). Densities of up to 200/m² have been recorded at Patonga, New South Wales (Branch & Branch, 1980). At this site *B. auratum* was absent from the low water mark of spring tides, and declined in numbers at higher levels. Although the snails were found grazing both on trunks and on the mud surface, they showed a preference for hard substrates and were most common on a belt of oysters.

Bembicium nanum is the only member of the genus which occurs on exposed rocky shores on mainland coasts, and even then is more frequent where wave action is reduced (Guiler, 1950, 1952b; H. Anderson, 1958; Bennett & Pope, 1960; Meyer & O'Gower, 1963; Underwood, 1975a). It is a dominant species of the upper eulittoral (barnacle or barnacle-limpet-mussel zone), and on rock platforms at Cape Banks, New South Wales, densities range from 19 to 205/m² (Meyer & O'Gower, 1963) or 70 to 160/m² (Underwood, 1975a, b). At this locality the distribution patterns have been analysed in detail. Underwood (1976a) found a homogeneous random dispersion with respect to patches of the encrusting alga *Peyssonelia* and shallow rock pools (although O'Gower & Meyer, 1971, reported reduced densities in pools), and a significantly aggregated dispersion on both bare rock and the alga (Underwood, 1976b). No seasonal changes in distribution were detected (Underwood, 1975b, 1976b).

The differences in the habitats of *Bembicium* species are such that syntopic occurrences are rare. Where mangroves occur on an ocean rock platform north of Sydney, *B. auratum* and *B. nanum* have been found together (Dakin, 1980: 248). These two

species also co-occur on the rocky shores of sheltered inlets, as in Port Stephens and Batemans Bay, New South Wales (AMS records), Port Jackson, New South Wales (pers. obs.) and Outer Harbour, Port Adelaide, South Australia (AMS records). In the mangroves of Western Port Bay, Victoria (pers. obs.) and on the sheltered rocky shores in southeastern Tasmania (TM records), *B. auratum* may be found together with *B. melanostoma*. Both *B. auratum* and *B. vittatum* occur in Oyster Harbour, southwestern Australia (Roberts & Wells, 1980; WAM records). *B. melanostoma* is occasionally found with *B. nanum* on rocky shores of moderate exposure in Port Phillip and Western Port Bays, Victoria (NMV records; pers. obs.) and in Tasmania (TM records). The segregation of *Bembicium* species is, however, normally so complete that they have been regarded as ecotypes of a single species (e.g. Guiler, 1952b). Differing tolerances of reduced salinity may partly account for the differences in habitats. In South Australia *B. nanum* and *B. vittatum* occur only in fully marine conditions, while *B. auratum* is found in estuaries and shows activity down to a 35% dilution of normal seawater (H. Anderson, 1958).

Differences in shell size within and between habitats have been noted by several authors. In *B. nanum*, larger individuals are found in positions exposed to stronger wave action, except under extreme exposure (Meyer & O'Gower, 1963; O'Gower & Meyer, 1965). On sandy or muddy flats in South Australia, shells of *B. vittatum* are smaller than on rocky shores (Womersley & Edmonds, 1958). A dwarf form of *B. auratum* occurs on high islands off the coast of northern Queensland. *B. nanum* shows a shore-level size gradient with juveniles in the upper parts of the range (Underwood, 1975a; Chilton & Bull, 1984), as is the case in many intertidal littorinids, of which juveniles are believed to inhabit the zone of minimal mortality (Vermeij, 1972). In contrast, Branch & Branch (1980) found juveniles of *B. auratum* in the lower part of the range, where survival may have been enhanced by the presence of a belt of oysters which provided a hard substrate, and where food levels were highest.

Little information is available on the predators of *Bembicium*. In New South Wales adult mortality is low (0.060 deaths/individual/month, Underwood, 1975a) and predation by crabs and large invertebrates is said to be insignificant (Underwood, 1978). On rocky shores in South Australia the crab *Ozius truncatus* is a predator of small snails and may be responsible for the maintenance of the observed shell size gradients (Chilton & Bull, 1984, 1986).

Bembicium nanum and *Nerita atramentosa* show significant segregation in their distributions on the shore, leading to the suggestion of interspecific competition between them (Underwood, 1976b). This has been confirmed by caging experiments, which also showed competitive effects from *Cellana*

tramoserica. The possibility of intraspecific competition for a limited supply of algal food has been demonstrated by caging *B. nanum* at two to four times the natural density, resulting in increased mortality and reduced flesh weight (Underwood, 1978). Similar caging experiments have shown intraspecific competition at densities greater than normal in *B. auratum*, and the correlation between chlorophyll levels in the substrate and natural snail density, together with depletion of chlorophyll in cages with high snail densities, suggest that food supply is the limiting resource (Branch & Branch, 1980).

There is relatively little information about the ecology of *Risellopsis varia* on New Zealand shores. It occurs in the upper eulittoral zone, in crevices amongst barnacles and *Modiolus* (Suter, 1913; Morton & Miller, 1968; Powell, 1979). The species attains a larger shell size in the southern parts of its range (Morton & Miller, 1968).

Reproduction, growth and population dynamics.

The reproductive seasons of *Bembicium* species show variation between localities, but in general the period of peak spawning is winter and spring. At Port Adelaide, South Australia, *B. auratum* produced egg masses in the laboratory from July to January (H. Anderson, 1958). At Middle Harbour, Sydney, egg masses of this species were found under stones in rock pools from August to December (D.T. Anderson, 1962). However, at Patonga, 50 km north of Sydney, a population spawned throughout the year, but with a peak in the numbers of mature gonads from April to September (Muggeridge, 1979). At some time during January to April each individual underwent a short period of total oocyte resorption, although this was asynchronous in the population as a whole. The males in this population contained sperm throughout the year, although in some individuals the testis, but not the penis, was reduced in size in January and February (Muggeridge, 1979). The breeding season of *B. vittatum* is not known, but egg masses have been recorded in the laboratory in October by H. Anderson (1958, as *B. melanostoma*), who suggested that the spawning period may have been earlier or shorter than in *B. auratum*.

Bembicium nanum has also been examined at several localities. At Harbord, north of Sydney, egg masses were found from October to April (D.T. Anderson, 1961), although Bedford (1965) reported continuous breeding in the vicinity of Sydney. A more detailed study by Underwood (1974) at Cape Banks, Botany Bay, demonstrated spawning from July to February, with reduction in size of the ovary from March to April or February to March. The testes were much reduced in size from March to May. At Balmoral, Port Jackson, Muggeridge (1979) recorded spawning by *B. nanum* from July to January, but without a synchronised rest period following spawning. The testes were enlarged for

most of the year, with some reduction from February to April, but the size of the penis was not reduced.

The breeding season of *Risellopsis varia* is not known, although veligers tentatively identified as this species have been recorded in plankton samples off Otago from January to April (Pilkington, 1976).

The factors controlling spawning in *Bembicium* species have not been investigated, although at least in *B. auratum* the onset of the major spawning period is associated with rising sea temperatures, and its cessation may be triggered by high summer temperatures (Muggeridge, 1979). The breeding cycles of both *B. auratum* and *B. nanum* show a correlation with the seasonal availability of phytoplankton as food for the veliger larvae (Underwood, 1974; Muggeridge, 1979).

As discussed above, *B. auratum*, *B. nanum* and *Risellopsis varia* hatch from benthic egg masses as planktonic veligers, while *B. vittatum* (H. Anderson, 1958, as *B. melanostoma*), and possibly also *B. melanostoma* and *B. flavescens*, are believed to lack a planktonic stage, undergoing direct development in the egg mass. The time from oviposition until hatching in *B. auratum* is ten days (Muggeridge, 1979, at 12 to 18°C; also D.T. Anderson, 1962), and in *B. nanum* 12 (D.T. Anderson, 1961) to 16 days (Bedford, 1966). The ultrastructure and cytochemistry of oogenesis and embryology of *B. nanum* have been described in detail by Bedford (1966). There is no information on the length of larval life; veligers of *B. auratum* have survived for 14 days in the laboratory (Muggeridge, 1979). D.T. Anderson (1961) kept veligers of *B. nanum* for four days, and described them as 'planktotrophic'. On the basis of the time lag between spawning and the appearance of 5 mm recruits in the size-frequency distribution of *B. nanum* on the shore, Underwood (1975a) suggested that this species might spend as long as one year in the plankton. This estimate was derived from the backward extrapolation of the constant rate of growth of juvenile cohorts. However, since the size of the protoconch of *B. nanum* indicates settlement at a diameter of 0.39 mm, the apparent lag period can be explained either by inadequate sampling of small juveniles or by rapid growth between settlement and appearance of 5 mm snails in the size-frequency histograms.

The shape of the protoconch of *Bembicium* species suggests a relatively short planktonic phase. In *B. auratum* this is supported by size measurements; the shell of the veliger 1.5 days before hatching, illustrated by D.T. Anderson (1962), measures 260 µm in diameter, which may be compared with a protoconch diameter, indicating size at settlement, of 350 µm. However, *B. nanum* appears to hatch at a smaller size; published figures of the veligers just before hatching show a shell size of 114 to 128 µm (Bedford, 1966) or 175 µm (D.T. Anderson, 1961), while the protoconch measures 390 µm. For comparison, the planktotrophic veliger of *Littorina*

scutulata grows from 160 µm at hatching to 300–360 µm at settlement in about three weeks (Buckland Nicks *et al.*, 1973). Newly hatched veligers of *Nodilittorina hawaiiensis* measure 110 to 120 µm and settle about 24 days later at a size of 250 µm (Struhsaker & Costlow, 1968, as *Littorina picta*, rearing temperature 25°C). Tropical *Littoraria* species grow from 100 to 140 µm at hatching to 320 to 415 µm at settlement, although the developmental time is not known (Reid, 1986). The size increment of *B. nanum* is similar to these, and the veliger presumably feeds in the plankton. By comparison, the veliger of *B. auratum* grows relatively little in the plankton and might even be non-planktotrophic. The relative size of the velum is, however, similar in *Bembicium* species (D.T. Anderson, 1961, 1962; Bedford, 1966) and in the planktotrophic *N. hawaiiensis* (Struhsaker & Costlow, 1968).

The suggestion of direct development in *B. vittatum* rests on the observation by H. Anderson (1958, as *B. melanostoma*) that embryos in the laboratory developed past the veliger stage, although they did not hatch from the egg capsules. Development of this species should be re-examined, and also in the closely related species *B. melanostoma* and *B. flavescens*.

Veligers of *Risellopsis varia* hatched from egg masses after 12 days at room temperature, with a shell 0.18 mm long (Pilkington, 1974). Similar veligers from plankton hauls off Otago measured 0.38 to 0.45 mm, but their identification was uncertain (Pilkington, 1976).

Bembicium auratum at Patonga, New South Wales, reached the maximum size of 16 to 19 mm shell diameter three years after settlement, at a mean growth rate of 0.58 mm per month (Muggeridge, 1979). Slow growth was also found by Branch & Branch (1980), who recorded increments in shell diameter of about 0.6 mm per month in juveniles at the same locality. Females showed slightly higher growth rates, maturing at a diameter of 12 mm, while males were mature at ten to 12 mm (Muggeridge, 1979). The population was dominated by adults, suggesting substantial juvenile mortality and high adult survival (Branch & Branch, 1980).

Analysis of polymodal size-frequency distribution has yielded a growth curve for *B. nanum* at Cape Banks. For the smallest cohort (I to 10 mm) growth in basal diameter was at a steady rate of 0.44 mm per month, reaching maturity at 11 mm. Instantaneous mortality rates were 0.233 deaths/individual/month for the juvenile cohort and 0.060 for adults, and longevity was estimated as four to eight years (Underwood, 1975a). Caging experiments at this locality demonstrated similar growth rates at three tidal levels, and showed that only near the upper limit of the vertical range was there insufficient food, or time for feeding, to permit maximal growth (Underwood, 1984).

Fossil Record

The generic name *Risella* was used by Cossmann (1915) for European fossils from as far back as the Triassic. However, his subgenus *Riselloidea* has been transferred to the archaeogastropod family Amberleyidae (Brookes Knight *et al.*, 1960) and his subgenus *Tanaliopsis* is regarded as a member of the Thiaridae (Kollmann, 1975). Two European Tertiary fossils have also been referred to *Risella* or *Bembicium*. These are *Trochus minutus* Deshayes (e.g. Cossmann, 1888, 1915; Glibert, 1962), and *Risella girondica* Benoist (Cossmann & Peyrot, 1919), both of which are members of the littorinid genus *Peasiella* (Reid, in prep.). *Tectarius rehderi* Ladd (Rosewater, 1972) bears a superficial resemblance to species of *Bembicium*, but is not a member of the genus (pers. obs. of type).

Fossil species of *Bembicium* are known only from New Zealand and Australia, and the earliest are of late Oligocene to early Miocene age. *B. priscum* Powell & Bartrum, described from the Otaian Stage (Lower Miocene) of New Zealand, probably occurs also in the Waitakian (basal Miocene) and the Lillburnian or Waiauan Stages (late Middle to early Upper Miocene). Also from the Otaian Stage are *B. discoideum* n. sp. and an unnamed species as yet known only from juveniles. A poorly preserved shell from the Altonian Stage (Lower Miocene) may represent an additional species. The only *Bembicium* known from the Tertiary of Australia is *B. altum* (Tate), which ranges from the Late Oligocene to Middle Miocene. As expected of intertidal molluscs found on hard substrates, fossils of *Bembicium* are rare.

Ludbrook (1984) has discussed the occurrence of the Recent *Bembicium* species in the Quaternary deposits of South Australia. Interestingly, although the genus is now extinct in New Zealand, it occurred there in the Pleistocene (Hutton, 1893; Suter, 1906, 1918; Speight, 1913; Finlay, 1923; Fleming, 1966). Previous authors have recorded these New Zealand fossils as *B. melanostoma*. However, without anatomical evidence even Recent shells of the *melanostoma* group can be difficult to distinguish. Four Pleistocene shells from the Castlecliffian Stage of the Wanganui area, New Zealand (NZGS) have been examined and all are rather worn (Fig. 24h). It can only be said that of the Recent species they most closely resemble the *melanostoma* group, and especially some specimens of *B. vittatum* from South Australia. *B. 'melanostoma'* has also been recorded from the Boat Cove Formation (Quaternary) of Raoul Island in the Kermadec Group (Marshall, 1981; specimen lost), to which the closest Recent occurrence is of *B. flavescens* at Norfolk Island.

Several Tertiary shells from New Zealand have been placed in the genus *Risellopsis*. These are *R. prisca* Powell and *Submargarita? tricincta* Marshall (Powell, 1935) and *R. gliscens* Marwick (1965). Maxwell (1969) has transferred the last to

Pterolabrella (Vitrinellidae), which seems appropriate for the others also (B. Marshall, pers. comm.; pers. obs.). The genus *Risellopsis* is represented only by the Recent species *R. varia*, of which there is but one known Pleistocene occurrence.

Biogeography

The genus *Bembicium* occurs only in mainland Australia, Tasmania and on Lord Howe and Norfolk Islands although, as discussed in the preceding section, there are fossil records from New Zealand and the Kermadec Islands. It is a typical and characteristic member of the endemic temperate molluscan fauna of the southern Australian region, and as such had its origin in the Australian - New Zealand element of the southeastern Australian Tertiary fauna (Darragh, 1985). Although the earliest fossils are from New Zealand, it is likely that the group originated in Australia, from which migration of most marine groups has proceeded eastwards (Knox, 1963).

On the basis of the distribution of intertidal organisms, seven biogeographical provinces have been recognised around the coast of the Australian mainland and Tasmania (Knox, 1963; Wilson & Gillett, 1971), although the boundaries between them are seldom sharply defined. Comparing the distributions of the *Bembicium* species with these biogeographical provinces, it can be seen that *B. melanostoma* is restricted to the cold temperate Maugean Province, being found only in Tasmania and on the mainland in Port Phillip and Western Port Bays. The western limit of the Maugean Province is at Robe, South Australia (Knox, 1963).

Bembicium nanum extends from Port Lincoln, South Australia, around the coasts of Victoria, Tasmania and New South Wales, having its northern limit at Yeppoon, Queensland (23°05'S). As noted by Underwood (1974), this is considerably north of the accepted boundary between the warm temperate Peronian and tropical Solanderian Provinces, at 25°S (Endean *et al.*, 1956). In contrast, the distribution of *B. auratum* includes that of *B. nanum*, and extends northward to Lizard Island (14°40'S). This species does, however, show geographical variation, with shells from northern Queensland being recognisably distinct from those from the more southerly parts of the range. Both northern and southern shell forms occur in Hervey Bay (25°S), with outlying northern forms (and intermediates) in Moreton Bay (27°S) and southern forms at One Tree Island (23°30'S). This agrees with the provincial boundary at 25°S and the northern affinities of Moreton Bay (Endean *et al.*, 1956). Records of *B. melanostoma* from Queensland (e.g. H. Anderson, 1958) are erroneous, and based on confusion with the northern form of *B. auratum*.

In southern Australia, the western limit of *B. nanum*, at Port Lincoln, is not a recognised biogeographical boundary. The most easterly record

of *B. vittatum*, at Port MacDonnell, is close to the boundary between the Flindersian and Maugean Provinces. In Western Australia, both *B. vittatum* and *B. auratum* reach their northern limit in the Houtman Abrolhos Islands (although the former is abundant, and the latter known from a single specimen and otherwise not further north than Perth). Wells (1980) found the sharpest change in the region of overlap between tropical and warm temperate molluscan faunas on the west coast to lie between Perth and the Houtman Abrolhos Islands.

Bembicium flavescens occurs only at Lord Howe and Norfolk Islands, as first noted by Etheridge (1889, as *Ricella* (sic) *plicatula*). Studying the chitons, Hedley & Basset Hull (1912) remarked on the similarity between the faunas of these islands, and the lack of relationship with Australia and New Zealand. However, Iredale (1914) considered that the biogeographical affinities of Lord Howe Island lay primarily with New Caledonia to the north, and that there was little similarity with Norfolk Island or the Kermadecs. This view was maintained by Iredale & Allen (1940), although they also pointed out the resemblances of the intertidal molluscs of Lord Howe, including *Bembicium*, to those of the Australian mainland. Knox (1963) classified Lord Howe and Norfolk Islands in separate biogeographical provinces, the Phillipian and Norfolkian respectively, although they had previously been joined in a single province (Dell, 1958).

The three species *B. melanostoma*, *B. vittatum* and *B. flavescens* are clearly very closely related and have in the past been considered synonymous (H. Anderson, 1958), since their shells may be of similar appearance. It is shown here that they are separable by their penial anatomy, and that their distributions do not overlap. *B. vittatum* may undergo direct development in benthic egg masses (H. Anderson, 1958, as *B. melanostoma*), and the protoconchs of *B. melanostoma* and *B. flavescens* suggest that they may have a similar development. The lack of a planktonic stage in all three species could explain their potential for isolation and allopatric speciation. It is surprising that *Bembicium* on Lord Howe and Norfolk Islands appear to be conspecific when separated by about 1000 kms of open ocean, but current patterns do not preclude circulation between the islands (see charts in Endean *et al.*, 1956) and might carry egg masses attached to floating debris. Populations of *B. melanostoma* exist on either side of Bass Strait, but there are no records of this species west of Port Phillip Bay, nor of *B. vittatum* east of Port MacDonnell in South Australia. The 400 km stretch of coastline between these points is one of exposed headlands and sandy beaches, which may be unsuitable for either species. No records of *Bembicium* species are available from the remote coast of the Great Australian Bight between Ceduna and Albany, explaining a gap in the distribution maps. It is

noteworthy that the lack of rocky substrates between Perth and Geraldton (Wells, 1980) has not prevented *B. vittatum* from reaching the Houtman Abrolhos Islands.

A number of authors have mistakenly recorded species of *Bembicium* in lists of Recent molluscs of New Zealand (Deshayes & Milne Edwards, 1843, as *Trochus melanostomus*; Dunker & Zelebor, 1866, and von Martens, 1873, both as *Risella kielmannsegi*; Hutton, 1878, as *Risella aurata*; Hutton, 1880, as *R. melanostoma*). Unless the Pleistocene records of *Bembicium* in New Zealand and the Kermadecs were only chance spatfalls, it is possible that extinction was caused by periodic subantarctic temperatures during the Pleistocene (see Beu, 1966; Marshall, 1981). Present day sea temperatures in New Zealand (Garner & Ridgway, 1965) and the Kermadecs (Marshall, 1981) are no cooler than those prevailing in Tasmania (Knox, 1963), where *Bembicium* is abundant. Since the molluscan fauna of the Kermadec Islands shows only weak affinity with that of New Zealand (Dell, 1958), it is likely that *Bembicium* reached the islands from Australia, via Norfolk Island.

Risellopsis varia is found throughout New Zealand and the Chatham Islands (Suter, 1913; Powell, 1979).

Relationships Within The Littorinacea

In the preceding sections describing the morphology of *Bembicium* and *Risellopsis*, the attempt has been made to assess character states as plesiomorphic or apomorphic with respect to other littorinacean taxa. However, it will be apparent that the choice of outgroup on which to base such decisions is unclear, and that in some cases the choice alters the conclusion. A detailed account of the phylogeny of the Littorinidae, and the relationships with other littorinacean families, is in preparation, but here it is appropriate to review briefly the current ideas, in the light of new information about *Bembicium* and *Risellopsis*.

The anatomy of a number of littorinid genera, including *Littorina*, *Melarhaphe*, *Cenchritis*, *Tectarius*, *Echininus*, *Nodilittorina* and *Littoraria*, is now fairly well known, as reviewed in the preceding sections and by Reid (1986). These 'typical' littorinids seem to form a natural group, united by the presence of sperm nurse cells, specialised penial glands or glandular discs, a generally open prostate, production of pelagic egg capsules, a complex spiral pallial oviduct with anterior bursa copulatrix and posterior seminal receptacle, and subepithelial albumen and capsule glands in the pallial oviduct, although some of these characters may be secondarily lost.

Unfortunately the anatomy of *Lacuna* and related genera is poorly known; only *L. pallidula* has been described in detail (Gallien & de Larambergue, 1938), although *L. vineta* is similar (pers. obs.).

Traditionally, these have been grouped as a separate family, the Lacunidae, on the basis of their umbilicate shells, low and subtidal habitat, pair of opercular tentacles, and radular characters. Ponder (1976) has pointed out that none of these characters is of significance at the family level, and has tentatively included the *Lacuna* group as a primitive subfamily of the Littorinidae. Other characters of this group which should be noted are the absence of sperm nurse cells, the presence of unspecialised subepithelial glands in the penis, the closure of the prostate, pallial vas deferens and penial sperm duct, the anterior bursa copulatrix, the absence of a seminal receptacle, the storage of sperm in the renal oviduct, the epithelial albumen glands in the multispiral pallial oviduct, and the absence of capsule glands. Several Antarctic genera, such as *Laevilitorina* and *Laevilacunaria*, appear to be intermediate between littorinids and lacunids in shell and radular characters (Ponder, 1976; Arnaud & Bandel, 1978), but almost nothing is known of their anatomy.

The affinities of the freshwater *Cremnoconchus* are doubtful. It is usually placed in the Littorinidae, although at least a separate subfamily may be desirable. Its anatomy has been described by Linke (1935), and characters include the absence of penial glands, the retraction of the penial filament, the closed prostate, pallial vas deferens and penial sperm duct, the anterior bursa copulatrix, the absence of a seminal receptacle, storage of sperm in the renal oviduct, and the multispiral pallial oviduct with capsule glands. It is not known whether sperm nurse cells are present.

Looking to more distantly related littorinaceans, the terrestrial Pomatiasidae (as represented by *Pomatias elegans*, described by Creek, 1951) show an absence of penial glands, a closed prostate, pallial vas deferens and penial sperm duct, no anterior bursa copulatrix, a widely open pallial oviduct, storage of sperm in the ovarian oviduct, opening of the renal oviduct into a posterior muscular chamber (possibly homologous with the seminal receptacle) and albumen and 'capsule' glands of the epithelial type.

The Eatoniellidae are believed to be primitive littorinaceans (Ponder, 1968; Ponder & Yoo, 1978) and are aphallate, with open pallial gonoducts in both sexes, no anterior bursa copulatrix, a posterior seminal receptacle for the storage of sperm and a pallial oviduct with epithelial glands.

The following tentative interpretation is suggested. With the Pomatiasidae and Eatoniellidae as outgroups, the family Littorinidae is defined by the synapomorphies of an anterior bursa copulatrix, closed pallial oviduct, and a spiral route of the egg groove within the pallial oviduct. There is no justification for separating the Bembiciidae as a separate family. From the available information *Bembicium* and *Risellopsis* together seem to form a distinct group within the Littorinidae, defined by the synapomorphies of the anterior salivary glands, the

anterior position of the junction of the duct of the seminal receptacle with the pallial oviduct, the longitudinal division of the jelly gland (shared with *Lacuna*) and shell shape (a convergence with *Peasiella*), and also by their Australasian distribution. This group could be recognised as a subfamily, to stand alongside Littorininae (synapomorphies of sperm nurse cells, mamilliform or disc-shaped penial glands, pelagic egg capsules, subepithelial albumen and capsule glands in pallial oviduct), and Lacuninae (loss of seminal receptacle, closed prostate). Confirmation or rejection of this scheme must await information on the anatomy of Antarctic littorinids, Arctic genera related to *Lacuna* and further details of *Cremnoconchus*. It is not at present possible to evaluate the relationships between these 'subfamilial' groups. Even from the brief descriptions given above, it will be seen that convergence of characters has occurred. The *Bembicium* group may appear to share characters with the Littorininae (seminal receptacle, open prostate), but these are synplesiomorphies.

Excluded Species

Brief accounts are given here of species which have been placed in the genera *Bembicium*, *Risella* or *Risellopsis* by previous authors, but which should now be excluded. Mesozoic fossils ascribed to *Risella* by Cossmann (1915) and Tertiary vitrinellids from New Zealand once placed in *Risellopsis*, have been discussed above.

Genus *Peasiella* Nevill, 1885

Shells of the littorinid genus *Peasiella* bear a close resemblance to those of *Bembicium* and *Risellopsis*. They are trochoidal and umbilicate, sculptured with spiral grooves, sometimes also with axial folds and peripheral crenulations, occasionally with periostracal hairs, and reach a maximum diameter of 6.6 mm. Well preserved shells can be distinguished from *Bembicium* by the form of the protoconch, which is 0.23 to 0.27 mm in diameter, of 2.0 to 2.2 whorls, sculptured by four wavy spiral ridges, and terminated by a marked sinusigera notch. The operculum is multispiral, unlike that of either *Bembicium* or *Risellopsis*. Anatomically, *Peasiella* is clearly separated by the vermiform penis, usually with a single penial gland, the form of the pallial oviduct (capsule glands are present, the bursa copulatrix vestigial or absent) and production of pelagic egg capsules. It is believed to be related to such typical littorinid genera as *Nodilittorina*, *Tectarius*, *Echininus* and *Cenchritis* (Reid, 1986). The genus *Peasiella* is widely distributed in the Indo-Pacific region, occupying crevices on rocks and mangroves, high in the intertidal zone.

Peasiella has in the past been considered a subgenus of *Risella* (e.g. Nevill, 1885; Tryon, 1887). Although given generic status by Thiele (1929) and

Wenz (1938), confusion still arises and the genus *Bembicium* is still sometimes used for the members of *Peasiella* (e.g. Glibert, 1962; Cernohorsky, 1978). A systematic account of *Peasiella* is in preparation, but meanwhile the available names for Recent species of the genus may be listed: *Margarita angulata* A. Adams, 1853; *Risella balteata* Preston, 1908; *Risella isseli* var. *carinata* Pallary, 1926; *Trochus conoidalis* Pease, 1868; *Trochus diminutivus* Reeve, 1862; *Cyclostrema fuscopiperata* Turton, 1932; *Echinella gaidai* Montrouzier, 1879; *Risella infracostata* Issel, 1869; *Risella isseli* Semper in Issel, 1869; *Risella isseli* var. *mauritanica* Viader, 1951; *Risella templiana* var. *nigrofasciata* Nevill, 1885; *Risella parvula* Dunker, 1861; *Risella roepstorffiana* Nevill, 1885; *Trochus sismondiae* Issel, 1869; *Risella templiana* var. *subimbricata* Nevill, 1885; *Risella tantillus* var. *subinfracostata* Nevill, 1885; *Trochus tantillus* Gould, 1849; *Risella templiana* Nevill, 1885; *Risella isseli* var. *undata* Pallary, 1926. The names of the Tertiary species of *Peasiella* include the following: *Xenophora bouryi* Cossmann, 1888; *Risella girondica* Benoist, 1874; *Trochus minutus* Deshayes, 1824; *Tornus orthezensis* Cossmann & Peyrot, 1915; *Xenophora pontileviensis* Morgan, 1915; *Pseudonina reyti* Cossmann & Peyrot, 1917; *Xenophora rhythida* Cossmann, 1900.

Risellopsis mutabilis May, 1909

The shell is superficially similar to that of *Risellopsis varia*, although with a more expanded last whorl and a groove outlining the umbilicus. The interior is greyish and does not appear nacreous, and the external colouration is purple black with two to three large, irregular white blotches at the shoulder

and suture of the final whorl in the largest shells (4 mm). The operculum is round and multispiral, the radula rhipidoglossate, and there are traces of epipodial tentacles (pers. obs., NMV F52213). The species is therefore a member of the Trochidae, and the genus *Fossarina* A. Adams & Angas, 1864 seems appropriate (A. Warén, pers. comm.).

Fossarus caledonicus Crosse, 1874

Although described as a *Fossarus*, this species has subsequently been placed in *Peasiella*, as a subgenus of *Risella* (Tryon, 1887; Kesteven, 1902). The shell bears superficial resemblance to *Peasiella* (see Crosse, 1875), but shows curious fine axial wrinkles, no spiral sculpture, a single strong basal rib, and a protoconch which suggests direct development. The operculum is round and multispiral. The radula is short and taenioglossate, with elongate, multicusped teeth. This species is believed to be a member of the Omphalotropinae (Assimineidae, Rissoacea) (W.F. Ponder, pers. comm.).

SYSTEMATIC DESCRIPTIONS

The range of intraspecific variation in shell characters in *Bembicium* is such that identification of unlocalised dry shells can be difficult or impossible. The following key therefore also makes use of anatomical characters and geographical distribution. For easier comparison, Table 1 lists the conchological characters of Recent *Bembicium* species. The key includes a short diagnosis of *Peasiella*, the range of which overlaps that of *Bembicium* in Queensland, and shells of which can easily be confused with juvenile *Bembicium*.

Table 1. Summary of shell characters of Recent *Bembicium* species.

Species	Radial folds, last whorl	Primary grooves, whorls 3-4	Total grooves, last whorl	Ridges on base, whorls 3-4	Ridges on base, last whorl	Columella colour	Aperture colour	Mean height/diameter ratio (\pm 95% confidence limits)
<i>B. melanostoma</i>	13-20	5	5-7	5-6	5-9	orange; (brown)	brown	0.855 \pm 0.020
<i>B. vittatum</i>	16-20 (12-25)	5-6	5-7(8)	5-6	7-9 (5-10)	orange, cream	brown, orange-brown	0.776 \pm 0.028
<i>B. flavescens</i>	14-23	5-6	5-7(9)	6-9	6-9	orange, (pink-brown)	brown	0.802 \pm 0.031
<i>B. auratum</i>	11-17 (9-21)	6-7	7-11 (6-12)	5	7-11	white, pale brown	cream or brown callus, usually 1-4 brown stripes at margin	0.965 \pm 0.024
<i>B. nanum</i>	15-20	4-5	7-9	3-4	4-7	white, pale orange	white, 4-10 brown stripes at margin, cream or brown callus	0.798 \pm 0.028

Parentheses indicate extremes of range.

Key to Recent species of *Bembicium* and *Risellopsis*

1. Shell small (< 6.6 mm diameter); protoconch 2.0–2.2 whorls, sculptured by 4 wavy spiral ridges; operculum multispiral; penis vermiform, usually with a single mamilliform penial gland; pallial oviduct lacks bursa copulatrix, capsule glands present. *Peasiella*
- Shell up to 28 mm diameter; protoconch 1.25–1.5 whorls, smooth; operculum paucispiral; penis broad, lacking penial glands; pallial oviduct with bursa copulatrix, capsule glands absent. 2
2. Shell < 8.3 mm diameter; 0–3 spiral ribs above peripheral keel, 4 on base; periostracum produced into bristles on ribs of well-preserved specimens; operculum paucispiral type B; New Zealand. *Risellopsis varia*
- Shell up to 28 mm diameter; 4–11 grooves above peripheral keel, 3–11 ridges on base; operculum paucispiral type A; Australia. (*Bembicium*) 3
3. 5–7 (rarely 9) spiral grooves above peripheral keel on last whorl; columella usually orange; aperture dark brown within. 4
- 7–12 spiral grooves above peripheral keel on last whorl; columella usually white, cream or brown; aperture cream or brown within, usually with black or brown and white stripes at margin. 5
4. 6–9 ridges on base of juveniles of 3–4 whorls; no umbilicus even in juveniles; apex sometimes blunt; penis Fig. 15a–h; Lord Howe and Norfolk Is. *B. flavescens*
- 5–6 ridges on base of juveniles of 3–4 whorls; umbilicus in juveniles only; penis Fig. 8; Tasmania and Victoria. *B. melanostoma*
- 5–6 ridges on base of juveniles of 3–4 whorls; umbilicus may persist in adult shells; penis Fig. 12; South and Western Australia. *B. vittatum*
5. 6–7 primary grooves on early whorls, 7–12 on last whorl; 7–11 ridges on base of last whorl; exterior often with dark nodules at periphery; penis Fig. 18. *B. auratum*
- 4–5 primary grooves on early whorls, 7–9 on last whorl; 4–7 ridges on base of last whorl; exterior with 18–38 oblique black lines, of which 4–10 are visible within margin of aperture; penis Fig. 15i–p. *B. nanum*

Genus *Bembicium* Philippi, 1846

Risella Gray, 1842: 60 [type species by subsequent designation (Gray, 1847) *Trochus melanostoma* Gmelin]. Here regarded as a *nomen oblitum*.

Bembicium Philippi, 1846: 130 [type species by subsequent designation (Herrmannsen, 1846) *Trochus melanostomus* (sic) Gmelin].

Diagnosis. Shell trochoidal, periphery usually keeled, base rather flat; small umbilicus in juveniles, usually closed in adults; within aperture of adults a thickened ridge present below peripheral keel. Protoconch smooth, 1.25–1.5 whorls, 0.35–0.40 mm diameter, sinusigera rib weak or absent. Teleoconch sculptured by spiral grooves and axial folds. Operculum paucispiral type A. Gonochoristic. Prostate an open groove; anterior vas deferens over head and through penis a closed tube; penis simple, opening of sperm duct subterminal, subepithelial glands absent. Sperm of one type only, nurse cells absent in seminal vesicle. Pallial oviduct comprises a single proximal spiral of albumen gland, and an

enlarged distal jelly gland, the latter divided into inner and outer chambers, capsule glands absent; opening into mantle cavity small and subterminal; 2 long separate ducts connect posterior seminal receptacle and renal oviduct to pallial oviduct, close to opening of the latter into mantle cavity; anterior bursa copulatrix. Benthic gelatinous egg masses; development either direct or planktotrophic. Radula littorinoid, each tooth bearing single major cusp and 2–3 smaller cusps, major cusps closely similar in size and shape in each tooth row, but variable within species. Salivary glands anterior to nerve ring around oesophagus.

Bembicium melanostoma (Gmelin, 1791)

Figs 3a,b, 7–9, 11e,f

Trochus in fauce nigerrimus Chemnitz, 1781: 29, pl. 161, figs 1526a,b*.

Trochus melanostoma Gmelin, 1791: 3581 [refers to Chemnitz, 1781: pl. 161, figs 1526a,b; neotype (H. Anderson, 1958: 554) SAM D14590, Furneaux Island

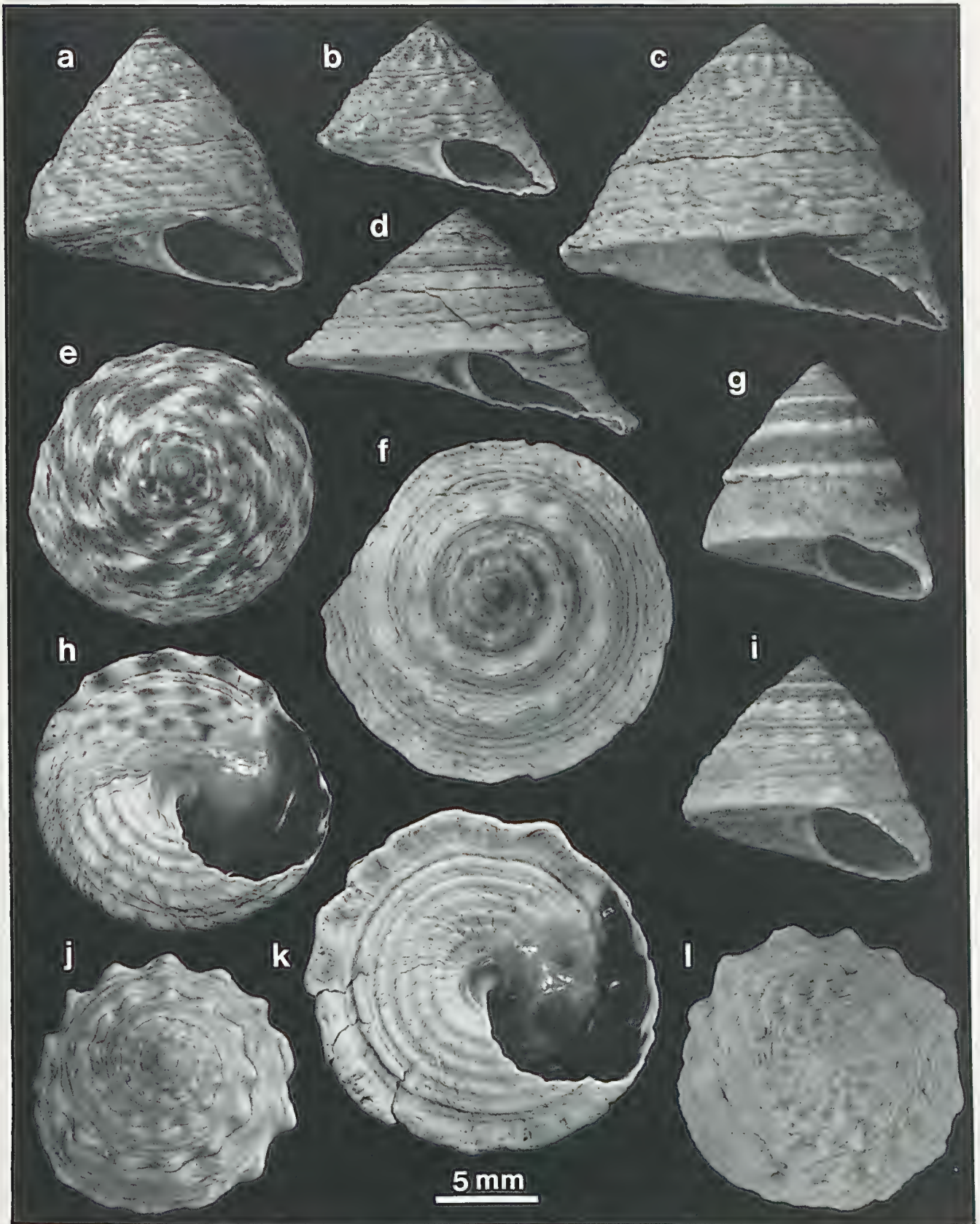


Fig.7. *Bembicium melanostoma* (Gmelin): a, Coal River estuary, south-east Tas. (TM E14479); b, Western Port Bay, Vic. (AMS C81871); c,d,f,k (3 views), Duck Bay, Smithton, Tas. (TM E14255); e,h (2 views), Cardinia Creek, Western Port Bay, Vic. (BMNH); g,i, Welcome River, Tas. (TM E15138); j, Crayfish Creek, Tas. (TM E5823); l, whitened to show sculpture, Western Port Bay, Vic. (AMS C81871).

- Group, Bass Strait, Australia].—Dillwyn, 1817: 797 *; Deshayes & Milne Edwards, 1843: 157–158 *.
- Bembicium melanostomum* (sic).—Philippi, 1846: 130 [in part]; Kershaw, 1955: 307; MacPherson & Gabriel, 1962: 90.
- Bembicium melanostoma*.—May, 1921: 48 [in part]; May, 1923: pl. 22, fig. 20; Wenz, 1938: 523, fig. 1380 *; MacPherson & Chapple, 1951: 118; H. Anderson, 1958: 553–558, pl. 2, figs 1, 2c [in part]; Ludbrook, 1984: 70, figs 20f–h, pl. 10j.
- Risella melanostoma*.—Gray, 1847: 150 *; Philippi, 1853: 8, pl. 1, figs 21, 22 [in part]; Adams & Adams, 1858: pl. 33, figs 5a–c*; Crosse, 1864: 229–233, pl. 11, fig. 1; Angas, 1865: 172 [in part]; Smith, 1884: 61–62 [in part]*; Tryon, 1887: 262–263, pl. 49, figs 20, 21, pl. 50, figs 30, 31 [in part]; Pritchard & Gatliff, 1902: 92–94 [in part].
- Littorina melanostoma*.—Tenison-Woods, 1879: 61–65 [in part].
- Trochus luteus* Quoy & Gaimard, 1834: 271–273, pl. 62, figs 8–11 [lectotype MNHNP, 15.2 x 15.8 mm, Port Western [Western Port Bay, Victoria, Australia] here restricted].
- Bembicium luteum*.—Philippi, 1846: 132 [in part]*.
- Risella lutea*.—Philippi, 1853: 4, pl. 1, figs 1, 2 [in part]*; Chenu, 1859: 302, fig. 2126*; Crosse, 1864: 237–239*; Fischer, 1879: 463, pl. 38, figs 2, 2a, 2b [in part]; Smith, 1884: 61–62 [in part]*.
- Trochus melanostoma* Reeve, 1842a: 185 [possible syntypes BMNH 1986074, 'coast of New Holland', here restricted to Tasmania].—Reeve, 1842b: 166, pl. 218, fig. 16.
- Bembicium lividum* Philippi, 1846: 131 [lectotype Philippi, 1853: pl. 1, fig. 27, New Holland]*.
- Risella livida*.—Philippi, 1853: 10, pl. 1, figs 27, 28*; Crosse, 1864: 240–241*.
- Trochus (Bembicium) squamiferus*.—Gould, 1852: 192, pl. 14, figs 227, 227a [not 'Koch' Philippi, 1844]*.
- Risella aurata*.—Tenison-Woods, 1877 [in part, not Quoy & Gaimard, 1934].
- Bembicium planum*.—Kershaw, 1955: 307 [not Philippi, 1846].

* references without adequate locality data may refer to either or both *B. melanostoma* and *B. vittatum*.

Nomenclature. The synonymy is complicated by the closely similar, and often indistinguishable, shells of *B. melanostoma* and *B. vittatum*. Published figures and most dry shells can only be identified with certainty when accompanied by locality data, since the two species are allopatric.

In his description of *Trochus melanostoma*, Gmelin refers to figures by Chemnitz (1781) of a shell collected by Cook in the 'South Seas'. The figures are poor, but the status of the species has been fixed by H. Anderson (1958), who designated as neotype a specimen from the Furneaux Island Group.

Quoy & Gaimard (1834) described *Trochus luteus*, and mentioned two localities in their text, Port du Roi-Georges (King George Sound, W.A.) and Port Western (Western Port Bay, Victoria). There are two syntypic lots in the MNHNP; one is labelled 'P.R.G.' (probably Port du Roi-Georges). The other,

unlocalised, includes the figured specimen (Quoy & Gaimard, 1834, pl. 62, fig. 8) which was also illustrated by H. Anderson (1958, pl. 2, fig. 2e). The shells in this lot resemble others from Western Port Bay more closely than the more depressed shells of *B. vittatum* from King George Sound. By designation of the figured specimen as lectotype, and restriction of the type locality to Port-Western, *Trochus luteus* is established as a synonym of *B. melanostoma*.

Reeve (1842a,b), apparently unaware of Gmelin's earlier use of the name, described *Trochus melanostoma* from 'New Holland'. Possible syntypes have been selected from the Cuming Collection in the BMNH, which resemble Reeve's figure. An original label accompanying the lot states the locality as Tasmania, and the type locality is fixed accordingly.

It should be noted that since '*melanostoma*' was used as a noun in apposition by Gmelin, the ending remains unchanged in combination with the generic name *Bembicium*.

Shell. (Fig. 7) DIMENSIONS. Adult size range 6.5–25 mm diameter; mean height/diameter ratio 0.855 (st. dev.=0.103, range 0.624–1.104, n=100 from 58 localities).

SHAPE. Teleoconch 5.5–7 whorls; shell of moderate thickness. Outline approximately equilaterally conical; sides lightly convex; base flat to slightly concave. Periphery strongly keeled, sometimes sharply flanged, but may become a little rounded on last whorl; sutures indistinct, unless preceding whorl is flanged. Small umbilicus in juvenile shells, becoming closed during fourth whorl. Ridge below peripheral keel in aperture is poorly developed.

SCULPTURE. Protoconch smooth, 0.40 mm diameter, 1.5 whorls, terminated by a growth line with no evidence of a sinusigera notch. First whorl of teleoconch marked by spiral striae and growth lines. On second whorl, 5 primary spiral grooves appear above periphery, 1–2 times the width of the rounded ribs between them; also on second whorl, radial folds appear, numbering 12–16 per whorl, and stretching from suture to periphery. Microsculpture of fine spiral threads, covering entire surface. Persistence of radial folds on subsequent whorls is variable; most commonly they become restricted to periphery, numbering 13–20 per whorl, and then obsolete on last 1–2 whorls, but sometimes persist, strongly crenulating periphery of last whorl, or may be absent after whorl 3. Spiral ribs and grooves persist, grooves are narrow and number 5–7 above periphery on last whorl, ribs a little narrower towards periphery. On larger whorls, microsculpture becomes oblique relative to spiral grooves, but remains perpendicular to the closely-spaced growth lines. On juvenile shells of 3–4 whorls, base is marked by 5–6 narrow spiral ridges, of which outermost is most prominent; a single additional ridge appears outside the prominent ridge, and single ridges in some inner

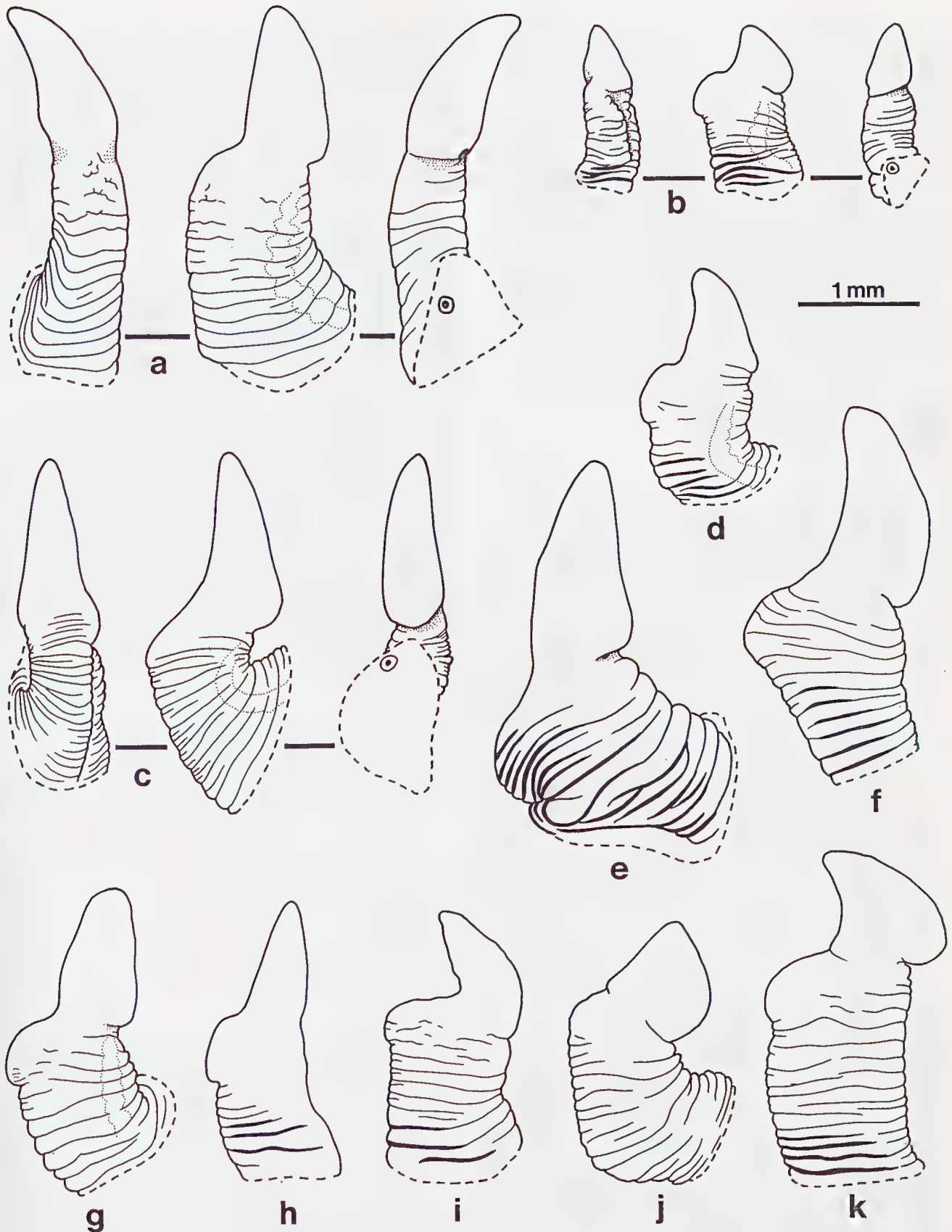


Fig.8. Penes of *Bembicium melanostoma* (Gmelin): a,c, Pittwater, 12 miles east-north-east Cambridge, Tas. (AMS C144404); b, Sidmouth, West Tamar River, Tas. (AMS C144332); d, Cremorne, Frederick Henry Bay, Tas. (AMS C144370); e, Eaglehawk Bay, Norfolk Bay, Tas. (AMS C144315); f, Brighton, Vic. (NMV F52230); g, Reidle Bay, Maria Island, Tas. (AMS C144403); h, Oyster Cove, Tas. (TME12523); i, Simpson's Bay, Bruni Island, Tas. (TME4860); j, Cat Bay, Phillip Island, Vic. (NMV F52207); k, Summerlands, Phillip Island, Vic. (NMV F5576); a,b,c, each show dorsal, lateral and ventral views (relative to orientation of head), all others are lateral views.

grooves, giving 5–9 subequal rounded ridges on base of last whorl; grooves between are 0.5–1 times rib width, marked by spiral microsculpture and close radial growth lines.

COLOUR. Shell cream to blue grey, peripheral folds or flange usually conspicuously paler; surface usually faintly flecked with darker grey, or occasionally with a dark purple brown pattern of irregular stripes and blotches. Eroded shells are black brown with a peripheral white stripe. Base commonly cream and unmarked, but sometimes with grey or brown flecks and spots on ribs. Columella almost always orange, sometimes orange brown or brown. Within aperture, area from suture to periphery is dark brown; base cream, parietal callus area cream to pale orange.

Animal. **PENIS** (Fig. 8). Filament $\frac{1}{3}$ – $\frac{1}{2}$ length of penis, laterally flattened, often elongate and curved away from opening of sperm duct, tip rounded; base lightly or not at all pigmented.

PALLIAL OVIDUCT (Fig. 3a).

RADULA (Fig. 11e,f). Length to 40 mm; relative length 1.93–2.67.

Distribution. **HABITAT.** Intertidal sand and mud flats in sheltered inlets; salt marshes and sometimes mangroves; eulittoral of sheltered rocky shores.

RANGE. (Fig. 9). Tasmania, Western Port and Port Phillip Bays, Victoria.

RECORDS. Victoria: Swan Bay (AMS, USNM); Portarlington (NMV); Williamstown (NMV,

USNM); Quail Island (NMV); Cardinia Creek, Western Port Bay (DGR); Cat Bay, Phillip Island (NMV); Palana, Flinders Island (TM); Tasmania: West Point, Marrawah (TM); Welcome River (TM); Duck Bay, Smithton (TM); Batman Bridge, Tamar River estuary (AMS); Sidmouth, West Tamar River (AMS); Mussel Roe Bay (TM); Cape Barren Island (TM); Coles Bay (TM); north side Reidle Bay, Maria Island (AMS); Pittwater, 12 miles east-north-east Cambridge (AMS); Eaglehawk Bay, south-east Norfolk Bay (AMS); Oyster Cove (TM); Simpsons Bay, Bruni Island (TM)

Remarks. The three species in the *melanostoma* group, *B. melanostoma*, *B. vittatum* and *B. flavescens*, are closely related. Shell characters which distinguish the group from the remaining two Recent species of *Bembicium* include the five to seven (sometimes up to nine) distinct spiral grooves above the periphery on the last whorl, five to nine ridges on the base of small shells of three to four whorls, and the colouration of the aperture, with a dark brown interior and orange columella. Although the combination of these features is characteristic, no single one is diagnostic (Table 1). Within the *melanostoma* group, *B. flavescens* can usually be distinguished by its smaller size, often blunt apex and lack of an umbilicus even in juveniles. The shells of *B. melanostoma* and *B. vittatum* are often inseparable, although a very small umbilicus is often



Fig. 9. Distribution of *Bembicium vittatum* Philippi (closed circles), *B. melanostoma* (Gmelin) (open circles), *B. flavescens* (Philippi) (open asterisks) and *Risellopsis varia* (Hutton) (closed asterisks).

present in adult shells of *B. vittatum*, but not in *B. melanostoma*. Also, the rather small, thin-shelled form of *B. vittatum* with a rounded periphery, found in sheltered bays in South Australia (described by Crosse as *Risella bruni*, e.g. Fig. 10j,k), is unique to this species.

The separation of the allopatric species *B. melanostoma*, *B. vittatum* and *B. flavescens* is based on consistent differences in penial shape. Since this may imply reproductive isolation, they are considered to be full species, rather than geographical subspecies, despite the close similarity of their shells. An electrophoretic analysis of isoenzymes would be desirable to test this conclusion. The 400 km stretch of coastline between the westernmost limit of *B. melanostoma* (Port Phillip Bay) and the easternmost limit of *B. melanostoma* (Port MacDonnell) is possibly too exposed for survival of either species. However, material of *Bembicium* species from this area in museums is limited and examination of this region for possible sympatric or intermediate populations would be desirable.

Bembicium melanostoma has been recorded as a Pleistocene fossil in New Zealand, but the available specimens are worn (e.g. Fig. 24h) and, in the absence of anatomical information, cannot be assigned with certainty to any of the three species of the *melanostoma* group.

Bembicium vittatum Philippi, 1846

Figs 9, 10, 11a-d, 12

Bembicium vittatum Philippi, 1846: 131 [lectotype Philippi, 1853: pl. 1, fig. 25; Adelaide, New Holland].—Cotton & Godfrey, 1938: 10.

Risella vittata.—Philippi, 1853: 9, pl. 1, figs 25, 26; Crosse, 1864: 241–242.

Risella fimbriata Philippi, 1851: 32 [no locality].—Philippi, 1853: 5–6, pl. 1, figs 9, 10 [lectotype fig. 9].

Risella bruni Crosse, 1864: 239–240, pl. 11, fig. 3 [syntypes BMNH 1870.10.26.152; Spencer Gulf, South Australia].—Angas, 1865: 173; Smith, 1884: 61.

Bembicium bruni.—Cotton & Godfrey, 1938: 10.

Risella lutea.—Fischer, 1879: 463 [in part, not Quoy & Gaimard, 1834].

Risella melanostoma.—Angas, 1865: 172 [in part, not Gmelin, 1791]; Tryon, 1887: 262–263, pl. 49, figs 15, 26–29 [in part, not Gmelin, 1791]; Pritchard & Gatliff, 1902: 92–94 [in part, not Gmelin, 1791]; Verco, 1908: 8 [not Gmelin, 1791].

Littorina melanostoma.—Tenison-Woods, 1879: 61–65 [in part, not Gmelin, 1791].

Bembicium melanostoma.—Hedley, 1916: 187 [not Gmelin, 1791]; H. Anderson, 1958: 553–558, pl. 1 fig. 2 (egg masses), pls 3–5 [a–c in part, not Gmelin, 1791].

Risella aurata.—Tenison-Woods, 1877 [in part, not Quoy & Gaimard, 1834].

Bembicium auratum.—Wells, 1980: 240 [not Quoy & Gaimard, 1834]; Wells & Bryce, 1986: pl. 10, no. 114 [not Quoy & Gaimard, 1834].

Note: refer also to synonymy of *B. melanostoma*.

Nomenclature. *Bembicium vittatum* and *B. melanostoma* cannot be reliably separated using shell characters alone; however, their geographical ranges are not known to overlap, and since Philippi gave the type locality 'Adelaide' for his species, the name *vittatum* can be associated with the western species of the *melanostoma* complex.

Philippi (1851) gave no locality for *Risella fimbriata*. This species is tentatively included in the synonymy of *B. vittatum* on the basis of the author's description of an open umbilicus, a feature which has not been seen in adult shells of *B. melanostoma*.

The shells described by Crosse (1864) as *Risella bruni* belong to a dwarf form of this species with rounded periphery and depressed outline, found in sheltered gulfs in South Australia.

Shell. (Fig. 10). DIMENSIONS. Adult size range 5.5–20 mm diameter; mean height/diameter ratio 0.776 (st. dev.=0.126, range 0.584–1.099, n=77 from 41 localities).

SHAPE. Teleoconch 5–7.5 whorls; shell of moderate thickness. Outline varies from low to equilaterally conical; sides lightly convex; base flat. Periphery strongly keeled, sometimes sharply flanged, but commonly becoming a little rounded on last whorl; sutures indistinct if whorls are flat, but clear in shells with slightly rounded whorls and in those with a prominent, undulating, peripheral flange. Small umbilicus present in juvenile shells, which often persists in adults. Ridge below peripheral keel within aperture is poorly developed.

SCULPTURE (Fig. 11a,b). Protoconch smooth, 0.37–0.45 mm diameter, 1.5 whorls, terminated by a growth line with no evidence of a sinusigera notch. First whorl of teleoconch marked by spiral striae and growth lines. On second and third whorls, 5–6 primary spiral grooves appear above periphery, approximately equal to width of the rounded ribs between them; also on third whorl, radial folds appear, numbering 11–17 per whorl, and stretching from suture to periphery. Microsculpture of fine spiral threads, covering entire surface. Persistence of radial folds on subsequent whorls variable; may remain prominent, numbering 16–20 (extremes of range 12–25) on last whorl, most well developed at periphery (especially shells from Houtman Abrolhos Islands), or more commonly become obsolete on last 1–3 whorls. Spiral ribs and grooves persist, grooves narrow, number 5–7 (rarely 8) above periphery on last whorl, ribs a little narrower towards periphery. On larger whorls, microsculpture becomes oblique relative to spiral grooves, but remains perpendicular to closely spaced growth lines. On juvenile shells of 3–4 whorls, base sculptured by 5–6 narrow spiral ridges, of which outermost most prominent; single ridges develop in some inner grooves to give 7–9 (extremes of range 5–10) subequal, rounded ridges on base of last whorl; grooves between are 1–3 times rib width, marked by spiral microsculpture and close

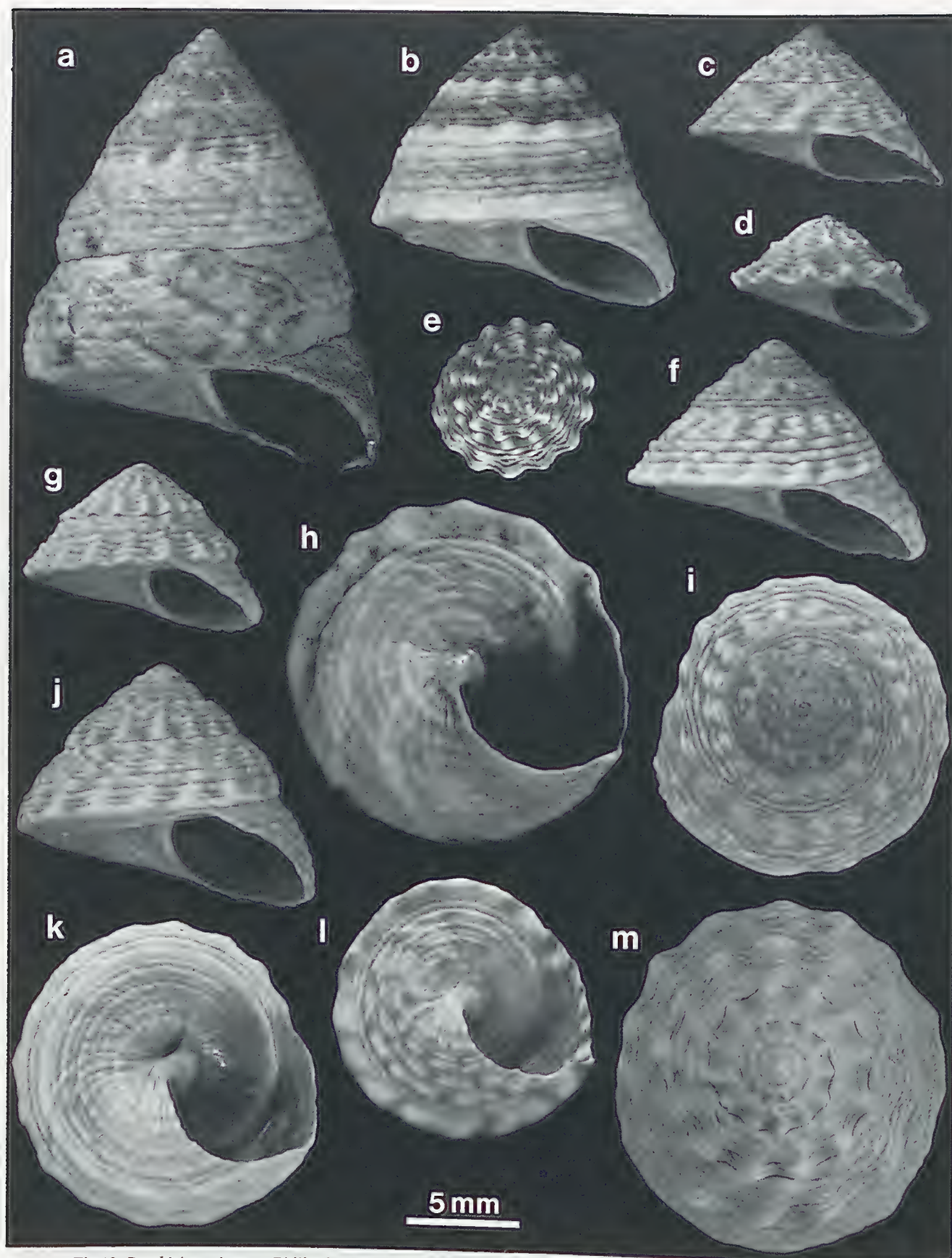


Fig.10. *Bembicium vittatum* Philippi: **a**, Port Lincoln, S.A. (SAM D17473); **b,h**, St Kilda, Adelaide, S.A. (AMS); **c,i**, (2 views), Salt Creek Bay, Yorke Peninsula, S.A. (SAM D17472); **d**, Mangrove Island, Abrolhos Islands, W.A. (WAM 421-85); **e**, Lusby Island, Sir Joseph Banks Group, S.A. (SAM D17474); **f,i** (2 views), **j,k** (2 views), Streaky Bay, S.A. (AMS C144305); **g**, Mangrove Island, Abrolhos Islands, W.A. (WAM N/1625); **m**, whitened to show sculpture, St Kilda, Adelaide, S.A. (AMS).

radial growth lines; ridges near umbilicus may be nodulose.

COLOUR. Shell cream to lilac grey, sometimes paler at suture or periphery; surface flecked and mottled with darker grey, occasionally with dark brown to black radial stripes in sculptural folds. Base may be unmarked or may bear brown flecks and spots on ribs. Columella orange or cream. Within aperture, area from suture to periphery is darkest, orange brown to dark brown; base cream; parietal callus area cream to pale orange.

Animal. PENIS (Fig. 12). Filament $\frac{1}{2}$ length of penis or greater, swollen, claw-shaped, pointed, with deep crease beside opening of sperm duct; base unpigmented or slightly so.

RADULA (Fig. 11c,d). Length to 35 mm; relative length 1.68–2.60.

Distribution. HABITAT. Intertidal sand and mud flats in sheltered inlets; salt marshes and mangroves; eulittoral of sheltered rocky shores.

RANGE (Fig. 9). From Port MacDonnell, South Australia, westward to Houtman Abrolhos Islands, Western Australia.

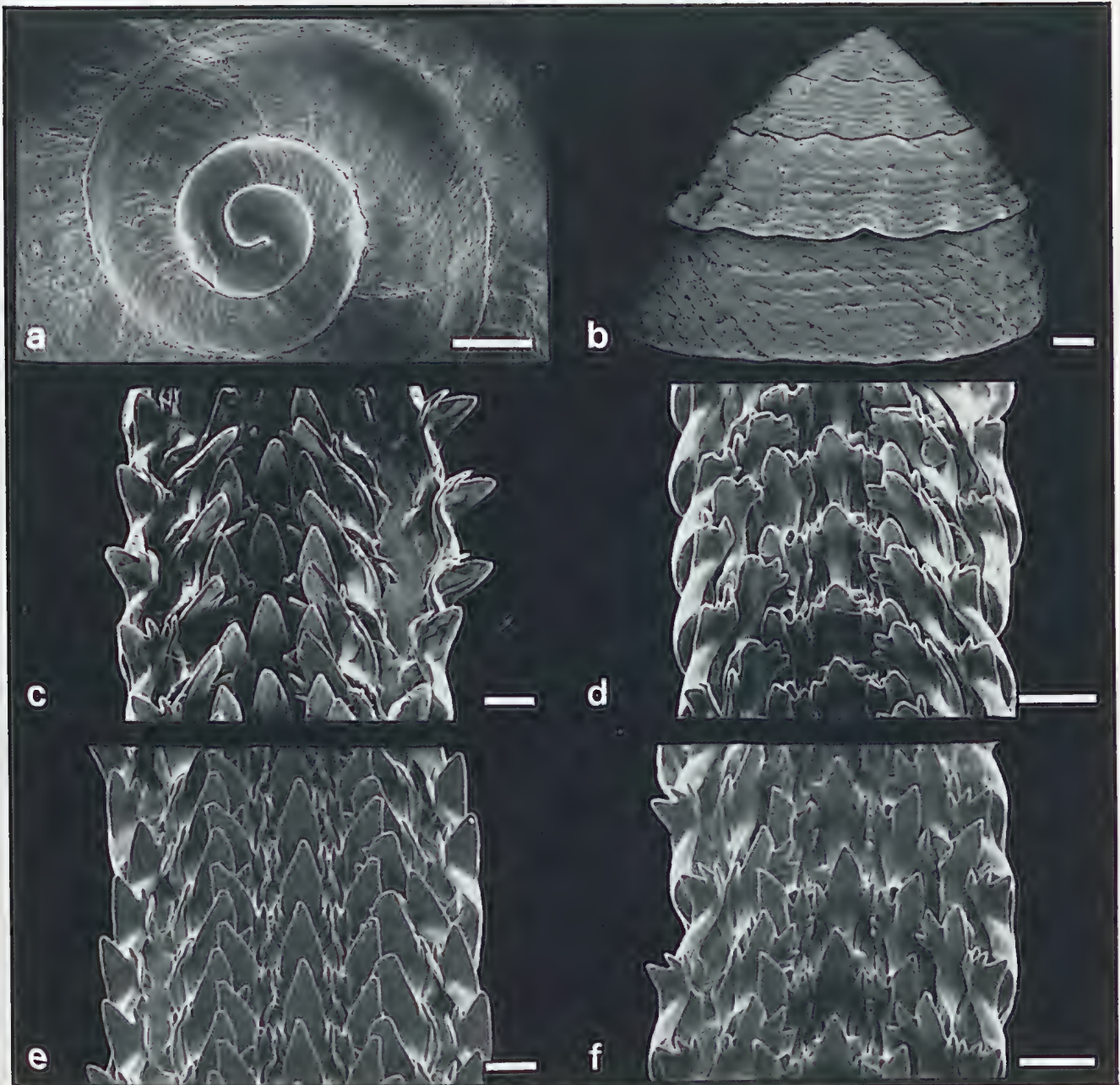


Fig. 11. *Bembicium vittatum* Philippi and *B. melanostoma* (Gmelin): a,b (2 views), *B. vittatum*, St Kilda, Adelaide, S.A. (AMS) (Bar a = 200 μ m, bar b = 1 mm); c, *B. vittatum* radula, Oyster Harbour, Albany, W.A. (AMS C144304); d, *B. vittatum* radula, Streaky Bay, S.A. (AMS C144305); e, *B. melanostoma* radula, Pittwater, 12 miles east-north-east Cambridge, Tas. (AMS C144402); f, *B. melanostoma* radula, Reidle Bay, Maria Island, Tas. (AMS C144403) (bar c–f = 50 μ m).

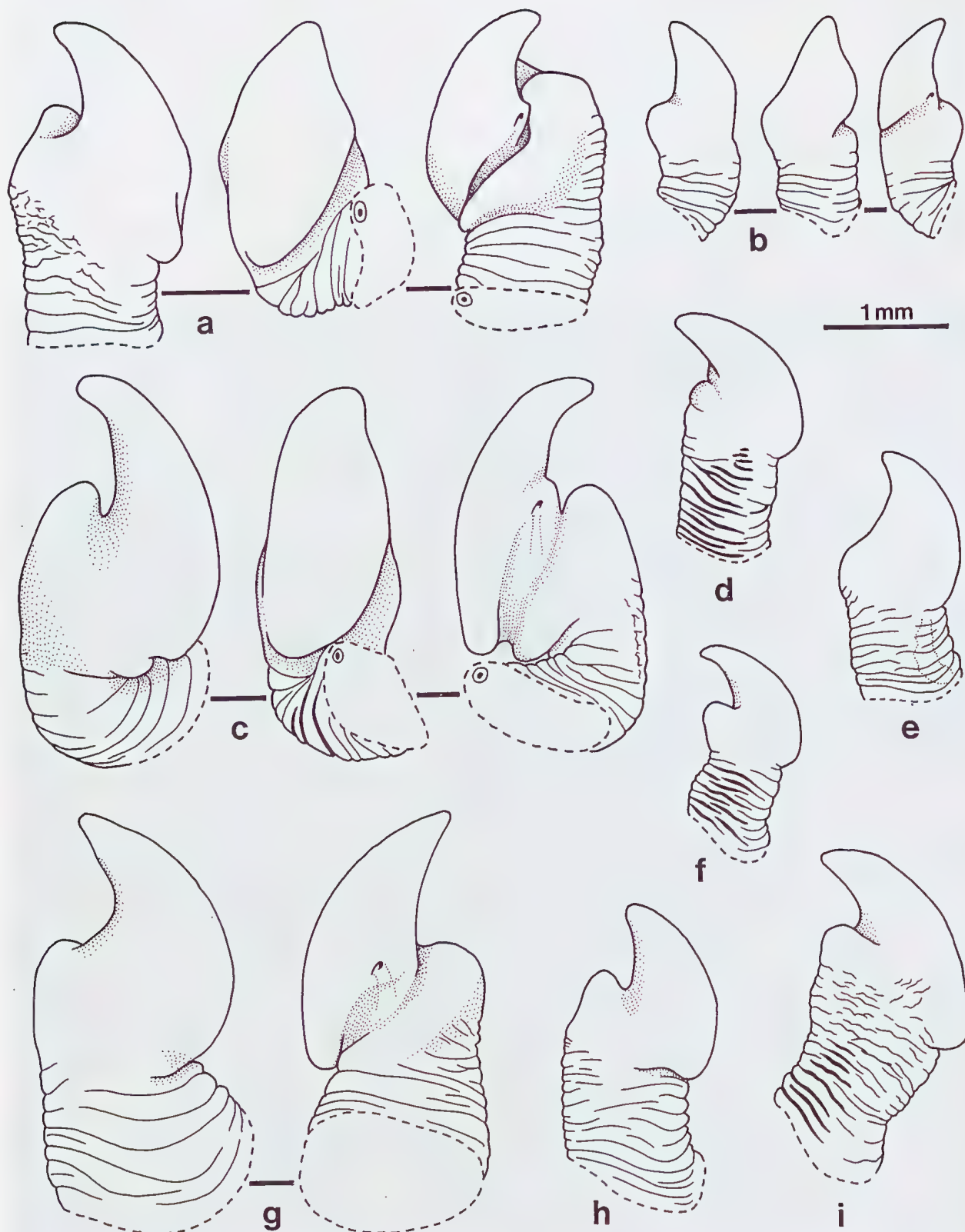


Fig. 12. Penes of *Bembicium vittatum* Philippi: a, c, Streaky Bay, S.A. (AMS C144305); b, Kalgan River, Albany, W.A. (AMS C144321); d, MacDonnell Bay, S.A. (AMS C144377); e, g, Oyster Harbour, Albany, W.A. (AMS C144304); f, Bay of Shoals, Kangaroo Island, S.A. (AMS C144375); h, Little Rat Island, Houtman Abrolhos Islands, W.A. (AMS); i, Pelican Lagoon, Kangaroo Island, S.A. (AMS C144378); a, b, c, each show lateral, ventral and medial views (relative to orientation of head), g, lateral and medial views, all others are lateral views.

RECORDS. South Australia: MacDonnell Bay (AMS); Port Willunga (SAM); St Kilda, Adelaide (AMS); Edithburg (AMS); Pelican Lagoon, American River, Kangaroo Island (AMS, SAM); Tumbly Bay (AMS); Lusby Island (AMS); Port Lincoln (AMS, SAM); Streaky Bay (AMS); Thevenard, near Ceduna (AMS); Western Australia: Oyster Harbour, Albany (AMS, WAM, BMNH); Penguin Island (WAM); Little Rat Island, Houtman Abrolhos Islands (AMS); Wooded Island, Houtman Abrolhos Islands (AMS, WAM).

Remarks. See remarks on *B. melanostoma*.

***Bembicium flavescens* (Philippi, 1851)**

Figs 9, 13, 14, 15a–h

Risella flavescens Philippi, 1851: 39 [Norfolk Island].—

Philippi, 1853: 7, pl. 1, figs 17, 18 [lectotype fig. 18].

Risella plicatula Philippi, 1851: 39–40 [Norfolk Island].—

Philippi, 1853: 9, pl. 1, figs 23, 24 [lectotype fig. 23].

Risella (sic) *plicatula*.—Etheridge, 1889: 24, 29.

Risella melanostoma.—Smith, 1884: 61–62 [in part, not Gmelin, 1791]; Tryon, 1887: 262–263, pl. 49, figs 22–25 [in part, not Gmelin, 1791].

Bembicium melanostoma.—H. Anderson, 1958: 553–558 [in part, not Gmelin, 1791].

Nomenclature. Like other species in the genus, *Bembicium flavescens* is variable in sculpture, and Philippi's species *Risella plicatula* is simply a strongly sculptured form. Both *R. flavescens* and *R. plicatula* were said by Philippi (1851) to have been seen in the collection of Hanley. However, neither is present amongst the material of Hanley in the Leeds City Museum (A. Norris, pers. comm.) and therefore the figures subsequently published by Philippi (1853) have been designated as lectotypes.

Shell. (Fig. 13). DIMENSIONS. Adult size range 4.5–16 mm, mean height/diameter ratio 0.802 (st. dev.=0.086, range 0.641–1.031, n=31 from 12 localities).

SHAPE. Teleoconch 4.5–6.5 whorls; shell moderately solid. Outline approximately equilaterally conical, apex sometimes blunt, sides lightly convex, base flat. Periphery strongly keeled, often crenulated by radial folds; sutures distinct if preceding whorl has crenulated periphery, giving turreted outline to spire. No umbilicus, even in juveniles of only 3 whorls. Within aperture, ridge below peripheral keel inconspicuous even in adults.

SCULPTURE (Fig. 14a–e). Protoconch smooth, 0.40 mm diameter, 1.5 whorls, terminated by growth line with no evidence of sinusigera notch. First whorl of teleoconch marked by growth lines and spiral striae of microsculpture. On second whorl, 5–6 wide primary spiral grooves appear above periphery, 1–3 times width of irregularly rounded ribs between them; grooves contain microsculpture of fine spiral threads; also on second whorl 13–17 radial folds appear, stretching from suture to periphery. On later whorls spiral grooves increase to 5–7 (rarely up to 9),

becoming narrower than the ribs between; ribs are rendered beaded or minutely nodulose by radial growth lines, and persist to last whorl. Microsculpture spreads over ribs as well as grooves, becoming somewhat oblique relative to spiral ribs. Radial folds increase to 14–23 per whorl, most prominent at periphery; folds may become obsolete on last 1–2 whorls, or may persist strongly. Although prominent, peripheral keel seldom conspicuously flanged even in juvenile shells. On juvenile shells of 3–4 whorls, base convex and marked by 6–9 fine spiral ridges, of which only outermost but one is prominent; on later whorls ridges become subequal and rounded, separated by shallow grooves approximately equal to rib width; grooves crossed by closely spaced growth lines and indistinct spiral microsculpture.

COLOUR. Upper half of each whorl blue grey, lower half white or cream; gaps between radial folds grey to dark brown or purple black, sometimes forming irregular radial stripes and blotches. Base white to cream, marked by scattered purple-brown spots on ribs, or irregular radial flames. Columella and parietal callus salmon orange to pinkish brown; aperture dark brown except for part below peripheral keel which is white.

Animal. PENIS (Fig. 15a–h). Filament $\frac{1}{2}$ – $\frac{1}{3}$ length of penis, laterally compressed, blade-shaped; side of base away from sperm duct produced into a finely wrinkled flange, base unpigmented.

RADULA (Fig. 14g,h). Length to 28 mm; relative length 2.19–3.05.

Distribution. HABITAT. Mid to upper eulittoral rock platforms; stones on muddy beach (Etheridge, 1889).

RANGE (Fig. 9). Lord Howe Island, Norfolk Island.

RECORDS. Lord Howe Island: Ned's Beach (AMS); Signal Point (AMS); Old Gulch (AMS); Norfolk Island: Point Hunter Reserve (AMS); Cascade (AMS); Anson Bay (AMS).

Remarks. See remarks on *B. melanostoma*.

It may seem surprising that *B. flavescens* occurs on both Lord Howe and Norfolk Island, separated by about 1000 km, especially if, as is possible, the species has direct development. The two populations are anatomically and conchologically indistinguishable, however. Electrophoretic studies could be carried out to determine the degree of genetic difference between the populations.

***Bembicium auratum* (Quoy & Gaimard, 1834)**

Figs 2, 3d, 4, 16–20

Trochus auratus Quoy & Gaimard, 1834: 276–277, pl. 62, figs 15–19 [lectotype MNHNP 21.3 x 25.1 mm; Entrecasteaux Channel, Van Diemen's Island [Tasmania]].

Risella aurata.—Crosse, 1864: 233–234; Angas, 1865: 173; Tenison-Woods, 1877 [in part]; Fischer, 1879: 462–463, pl. 34, figs 2, 2a.

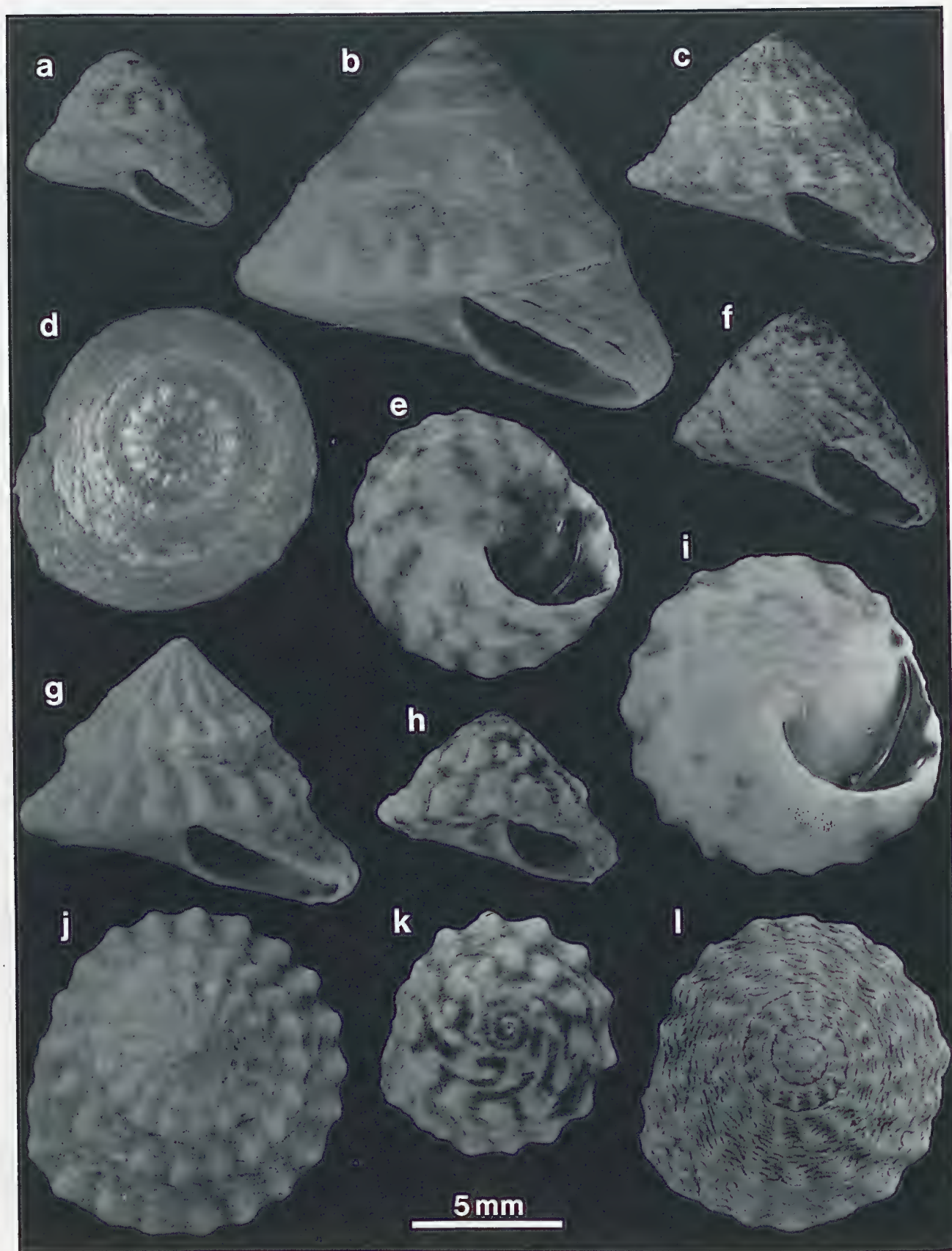


Fig.13. *Bembicium flavescens* (Philippi): a,c,e,f (2 views), h,k (2 views), Signal Point, Lord Howe Island (AMS C144350); b,g,j (2 views), Ned's Beach, Lord Howe Island (AMS C144404); d, Cascade, Norfolk Island (AMS C144354); i, Point Hunter Reserve, Norfolk Island (AMS C144401); l, whitened to show sculpture, Signal Point, Lord Howe Island (AMS C144350).

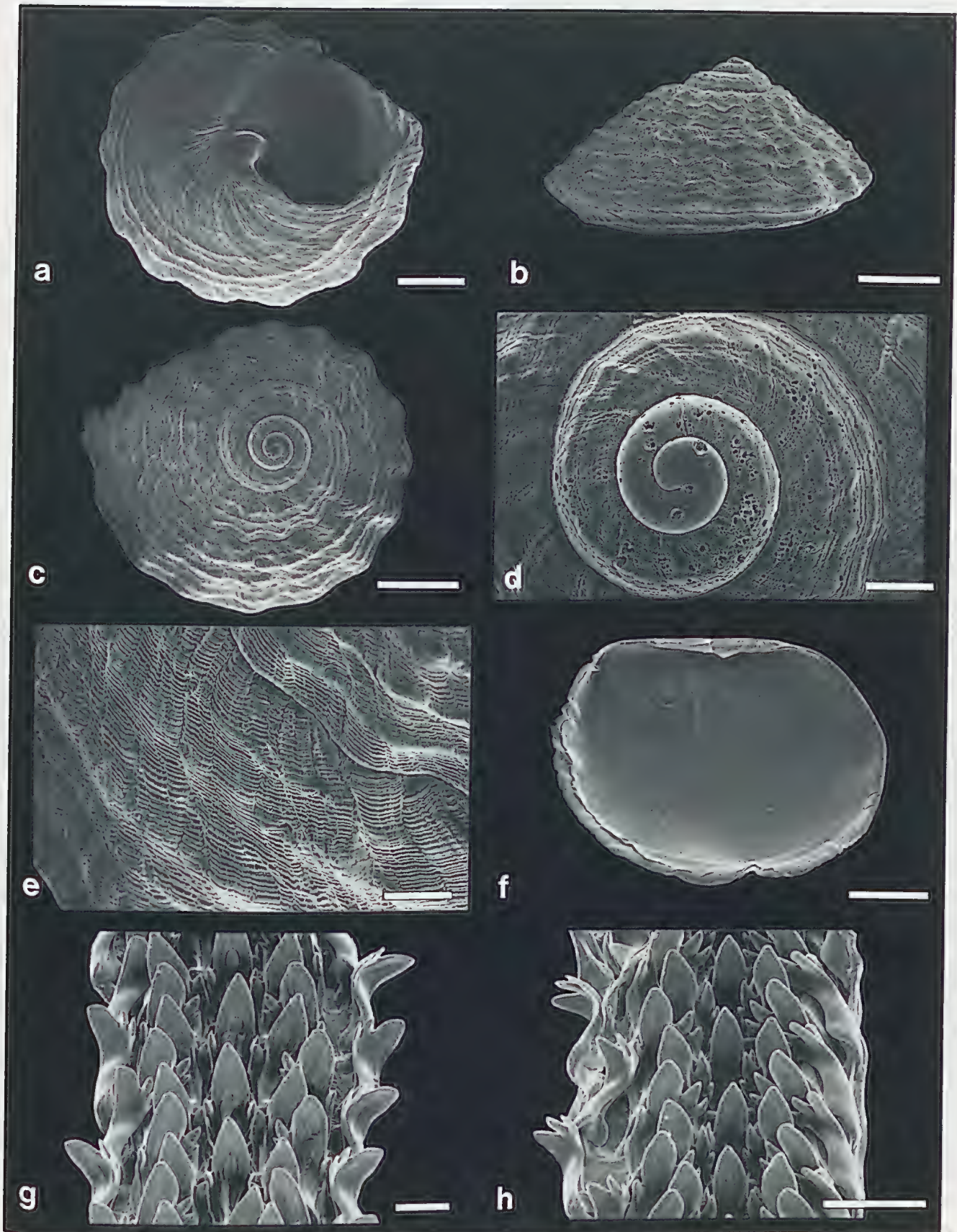


Fig.14. *Bembicium flavescens* (Philippi): a,b-e (4 views), juveniles, Signal Point, Lord Howe Island (AMS C144350) (bars a-c = 1 mm, bars d,e = 200 μ m); f, operculum, Ned's Beach, Lord Howe Island (AMS C144404) (bar = 1 mm); g, radula, Point Hunter Reserve, Norfolk Island (AMS C144401); h, radula, Signal Point, Lord Howe Island (AMS C144350) (bars g,h = 50 μ m).

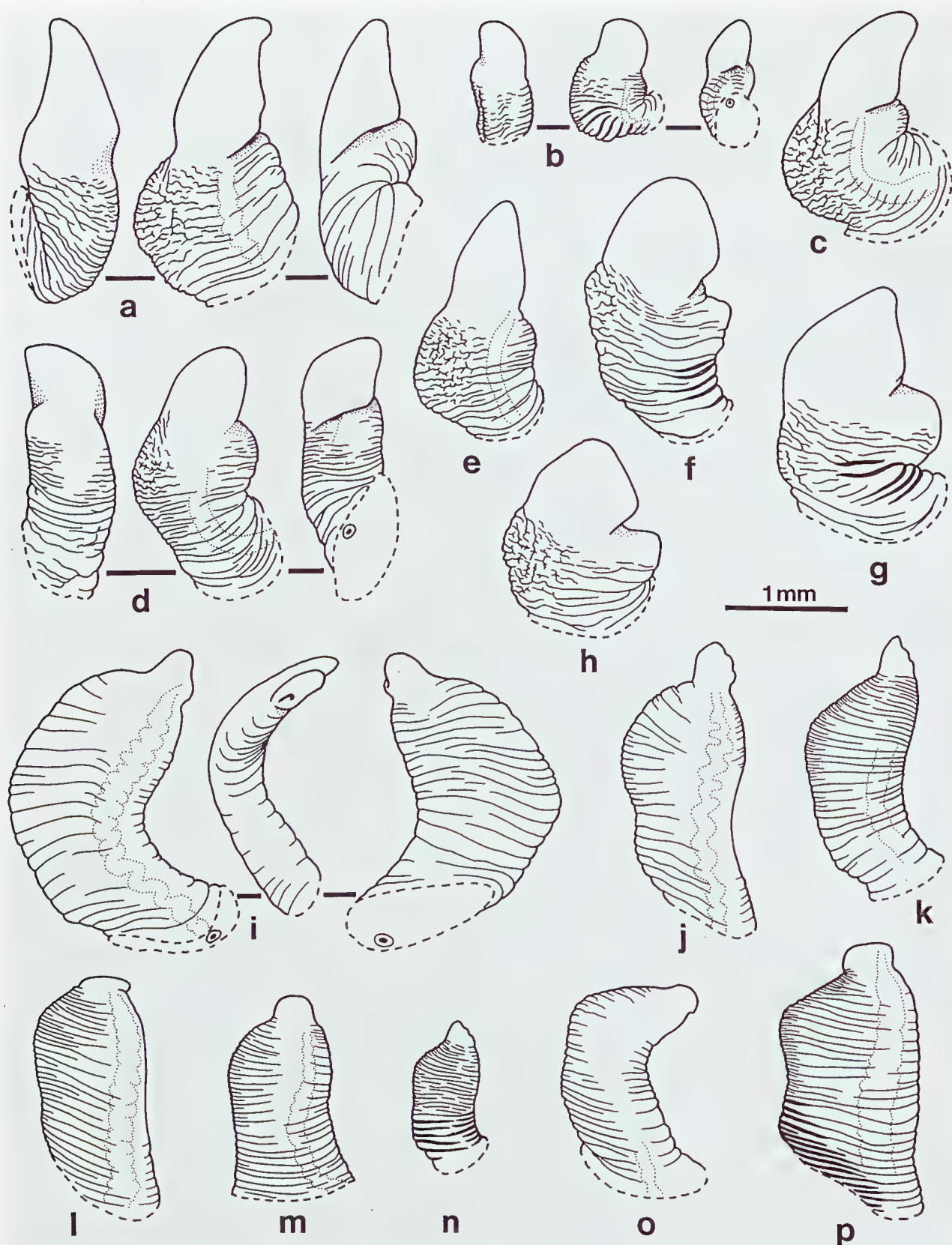


Fig. 15. a–h, penes of *Bembicium flavescens* (Philippi): a, Lord Howe Island (AMS C144294); b, Signal Point, Lord Howe Island (AMS C144350); c, d, e, Ned's Beach, Lord Howe Island (AMS C144404); f, g, h, Point Hunter Reserve, Norfolk Island (AMS C144401); i–p, penes of *Bembicium nanum* (Lamarck): i, j, Flinders, Vic. (AMS C144314); k, m, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); l, Yeppoon, Qld. (AMS C144338); n, Devonport, Tas. (AMS C144418); o, Normanville, S.A. (AMS); p, Pirates Bay, Eaglehawk Neck, Tas. (AMS C144334); a, b, d, each show dorsal, lateral and ventral views (relative to orientation of head), i, lateral, ventral and medial views, all others are lateral views.

Bembicium auratum.—MacPherson & Chapple, 1951: 118; H. Anderson, 1958: 560–565, fig. 1 (pallial oviduct), pl. 1, fig. 1 (vas deferens), fig. 3 (egg masses), pl. 2, figs a,b, pls 3–5 g, h; Dakin, 1960: 248, pl. 61, fig. 5; D.T. Anderson, 1962: 62–63, figs 1–6 (larval development); MacPherson & Gabriel, 1962: 89–90, fig. 118; Wilson & Gillett, 1971: 30, pl. 11, figs 13, 13a; Fretter, 1982 (anatomy); Ludbrook, 1984: 70, figs 20c–e.

Littorina imbricata Gray, 1839: 141 [lectotype BMNH 1968366, 16.4 x 17.9 mm; no locality].

Bembicium imbricatum.—Philippi, 1846: 132–133; Cotton & Godfrey, 1938: 10.

Risella imbricata.—Philippi, 1853: 4–5, pl. 1, figs 4, 5; Troschel, 1856–63: 137, pl. 11, fig. 8 (radula); Crosse, 1864: 242–243; Smith, 1884: 61–62; Nevill, 1885: 158.

Trochus cicatricosus 'Jonas' Philippi, 1843: 66, *Trochus* pl. 2, fig. 2 [type lost; New Holland].

Bembicium melanostoma.—Philippi, 1846: 130 [in part, not Gmelin, 1791]; Hedley, 1918: M51 [not Gmelin, 1791]; May, 1921: 48 [in part, not Gmelin, 1791]; H. Anderson, 1958: 553–558 [in part, not Gmelin, 1791]; Wells, 1980: 240 [not Gmelin, 1791]; Wells & Bryce, 1986: pl. 10, no. 112 [not Gmelin, 1791].

Risella melanostoma.—Philippi, 1853: 8 [in part, not Gmelin, 1791]; Chenu, 1859: 302, fig. 2127 [not Gmelin, 1791]; Tryon, 1887: 262–263, pl. 49, figs 3–9 [in part, not Gmelin, 1791]; Pritchard & Gatliff, 1902: 92–94 [in part, not Gmelin, 1791]; Hedley, 1910: 355 [not Gmelin, 1791].

Littorina melanostoma.—Tenison-Woods, 1879: 61–65 [in part, not Gmelin, 1791].

Bembicium luteum.—Philippi, 1846: 132 [in part, not Quoy & Gaimard, 1834].

Risella lutea.—Philippi, 1853: 4 [in part, not Quoy & Gaimard, 1834]; Adams & Adams, 1858: pl. 33, fig. 5 [not Quoy & Gaimard, 1834]; Angas, 1867: 209 [not Quoy & Gaimard, 1834]; Smith, 1884: 61–62 [in part, not Quoy & Gaimard, 1834]; Nevill, 1885: 159 [in part, not Quoy & Gaimard, 1834].

Risella kielmannsegi Zelebor in Dunker & Zelebor, 1866: 913 [type not seen; 'New Zealand' in error, probably Botany Bay, New South Wales, H. Anderson, 1958: 562]. —Frauenfeld, 1867: 9, pl. 1, figs 11 a–e.

Bembicium kielmannsegi.—Iredale, 1936: 289; Allan, 1950: 81, fig. 19, no. 5; Dakin, 1953: 248, pl. 61, fig. 5; Iredale & McMichael, 1962: 39.

Bembicium nodulosum Musgrave, 1929: 344 [*lapsus*, Iredale, 1936: 289]. —Iredale, 1931: 208–209.

Nomenclature. The tall spire and nodulose sculpture make this species readily recognisable, so that published figures can usually be identified.

Risella kielmannsegi was described from New Zealand, but as pointed out by H. Anderson (1958) the Novara Expedition also called at Botany Bay, and this is the likely origin of the specimens. Suter (1906, 1913) suggested that *R. kielmannsegi* was based on young *Astraea sulcata*, but Frauenfeld's excellent figures leave no doubt that the species is *Bembicium auratum*.

Shell. (Fig. 16) **DIMENSIONS.** Adult size range 5–28 mm diameter; mean height/diameter ratio 0.965 (st. dev. = 0.120, range 0.639–1.483, $n = 100$ from 36 localities).

SHAPE. Teleoconch 6.5–8 whorls; apical whorls commonly eroded; shell thick. Outline approximately equilaterally conical or taller; sides straight to lightly convex; base flat to slightly convex. Periphery strongly keeled in juveniles, becoming somewhat rounded on last whorl and bearing strong, blunt nodules. In shells from north Queensland keel marked by strong undulating flange throughout. Sutures indistinct, unless preceding whorl flanged. Small umbilicus in juvenile shells, becoming closed after third whorl. Within aperture of adults thickened ridge present below peripheral keel.

SCULPTURE. (Fig. 17a–g). Protoconch smooth, 0.35 mm diameter, 1.25 whorls, terminated by growth line with slight sinusigera notch. First whorl of teleoconch marked by faint spiral striae and growth lines. Beginning on second whorl, and more clearly by third, 6–7 primary grooves appear above periphery, equal in width to beaded ribs between them. Microsculpture of fine spiral threads at first distinct only in grooves, but after whorl 3 over whole surface. During second whorl radial folds appear, numbering 11–15 per whorl, stretching from suture to periphery, but prominence and persistence of radial folds variable. Typically folds remain prominent near suture and especially towards periphery of all succeeding whorls, numbering 11–17 per whorl (extremes of range 9–21). In some shells (especially those from north Queensland), radial folds become almost obsolete after whorl 3, remaining only as indistinct undulations of peripheral flange. Spiral sculpture persists, of 7–11 (extremes of range 6–12) narrow grooves on last whorl; ribs appear beaded or minutely scaly where crossed by radial growth lines. On last whorl microsculpture becomes oblique relative to spiral ribs. On juvenile shells of 3–4 whorls, base marked by 5 sharp spiral ridges, of which outermost is most prominent; further ridges soon appear, giving a total of 7–11 subequal grooves on base of last whorl, separated by grooves similar in width. Closely spaced radial growth lines and spiral microsculpture cover base.

COLOUR. Shell from entirely cream to brown. Juveniles either entirely brown, or with brown colour between radial folds. In adults brown colour forms broad, irregular, axial stripes corresponding to the radial folds, becoming more prominent in eroded shells. Shells from north Queensland may lack brown colour. Base with irregular dashes and spots of brown on spiral ridges. Columella white to pale brown. Aperture commonly cream with black pattern near margin, corresponding to stripes of exterior, becoming obscured by cream or dark brown callus within; aperture may, however, be entirely cream (especially in shells from north Queensland) or blackish brown.

Animal. (Fig. 2). **PENIS** (Fig. 18). Filament approximately half length of penis, swollen, irregularly hammer-shaped, tip usually rounded,

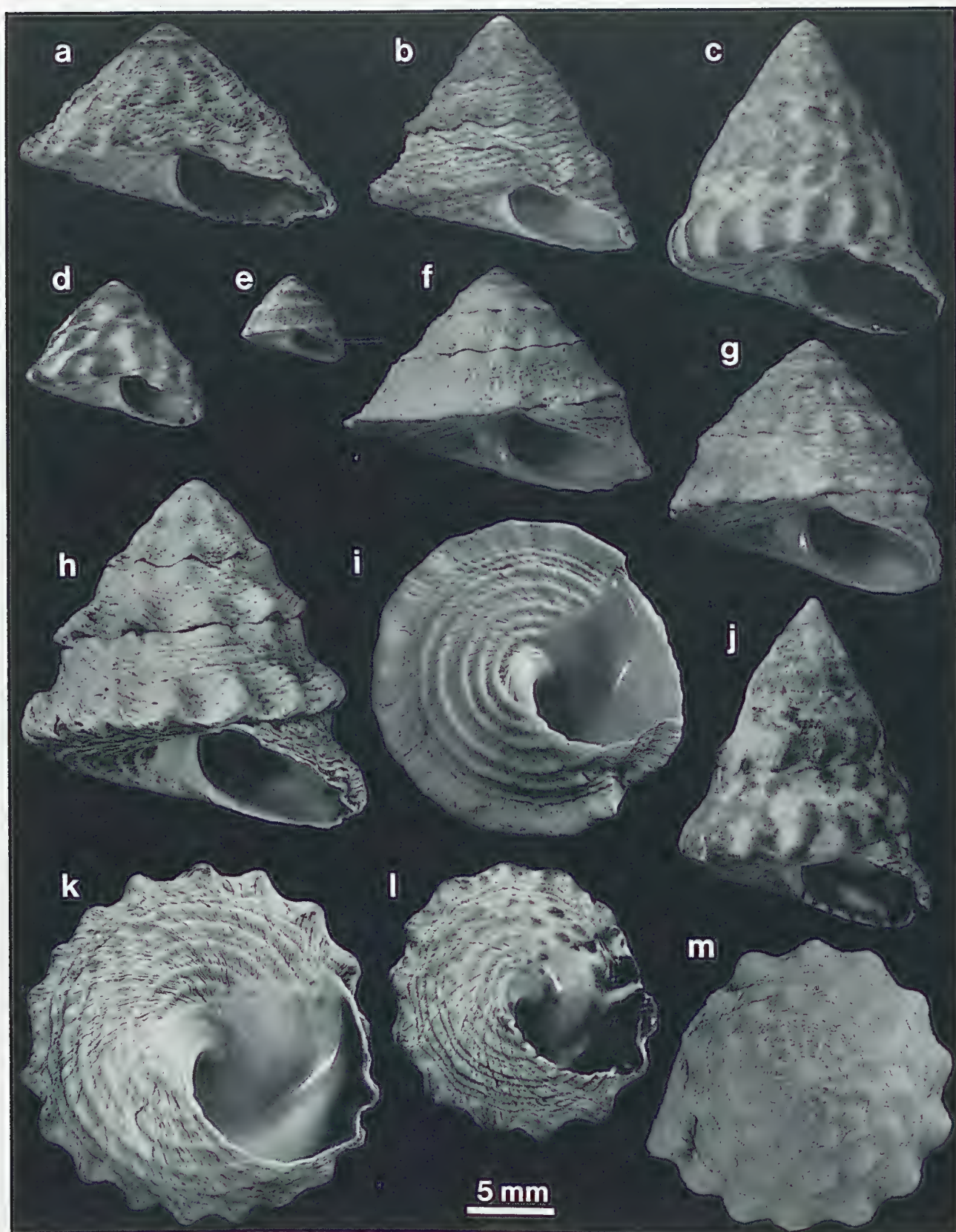


Fig.16. *Bembicium auratum* (Quoy & Gaimard): a, Point Perpetua, Sarina Beach, Qld (AMS C144373); b, Eurimbula Creek, south of Bustard Head, Qld (AMS C144286); c, Oyster Harbour, Albany, W.A. (AMS C144304); d, North Keppel Island, Qld (AMS C144367); e, Shute Island, Whitsunday Islands, Qld (BMNH); f,i (2 views), Proserpine River estuary, Wilson, Qld (AMS C144335); g, Campwin, south of Mackay, Qld (BMNH); h,k (2 views), Western Port Bay, Vic. (AMS C144357); j,l, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); m, whitened to show sculpture, Western Port Bay, Vic. (AMS C144357).

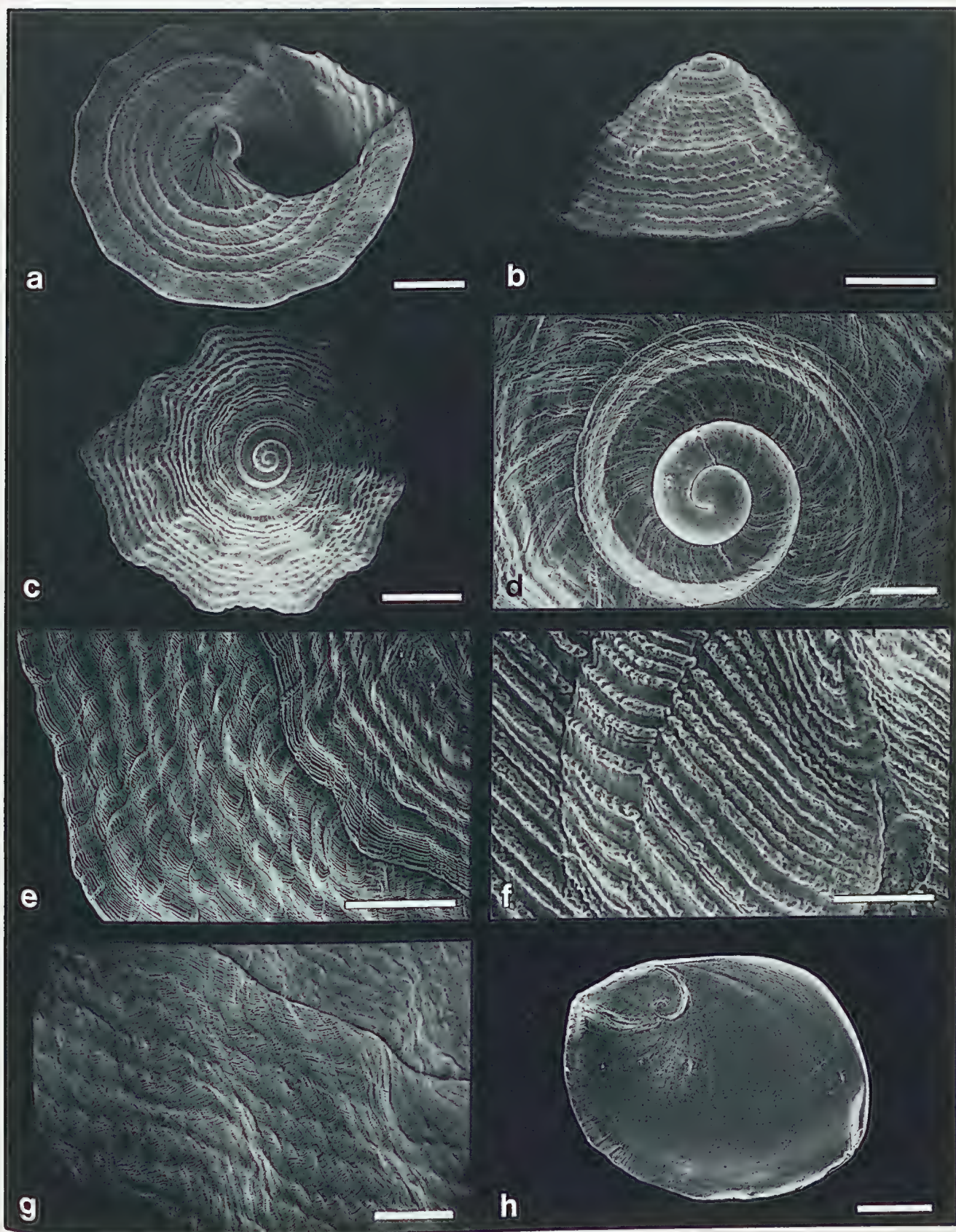


Fig. 17. *Bembicium auratum* (Quoy & Gaimard): **a**, juvenile, Iluka, N.S.W. (AMS C144387) (bar = 500 µm); **b–f** (5 views), juvenile, Urangan, Qld (AMS C144275) (bars **b**, **c** = 1 mm; bar **d** = 200 µm; bar **e** = 500 µm; bar **f** = 50 µm); **g**, sculpture of last whorl, Stradbroke Island, Qld (AMS C144347) (bar = 1 mm); **h**, operculum, Bateman's Bay, N.S.W. (AMS C144364) (bar = 1 mm).

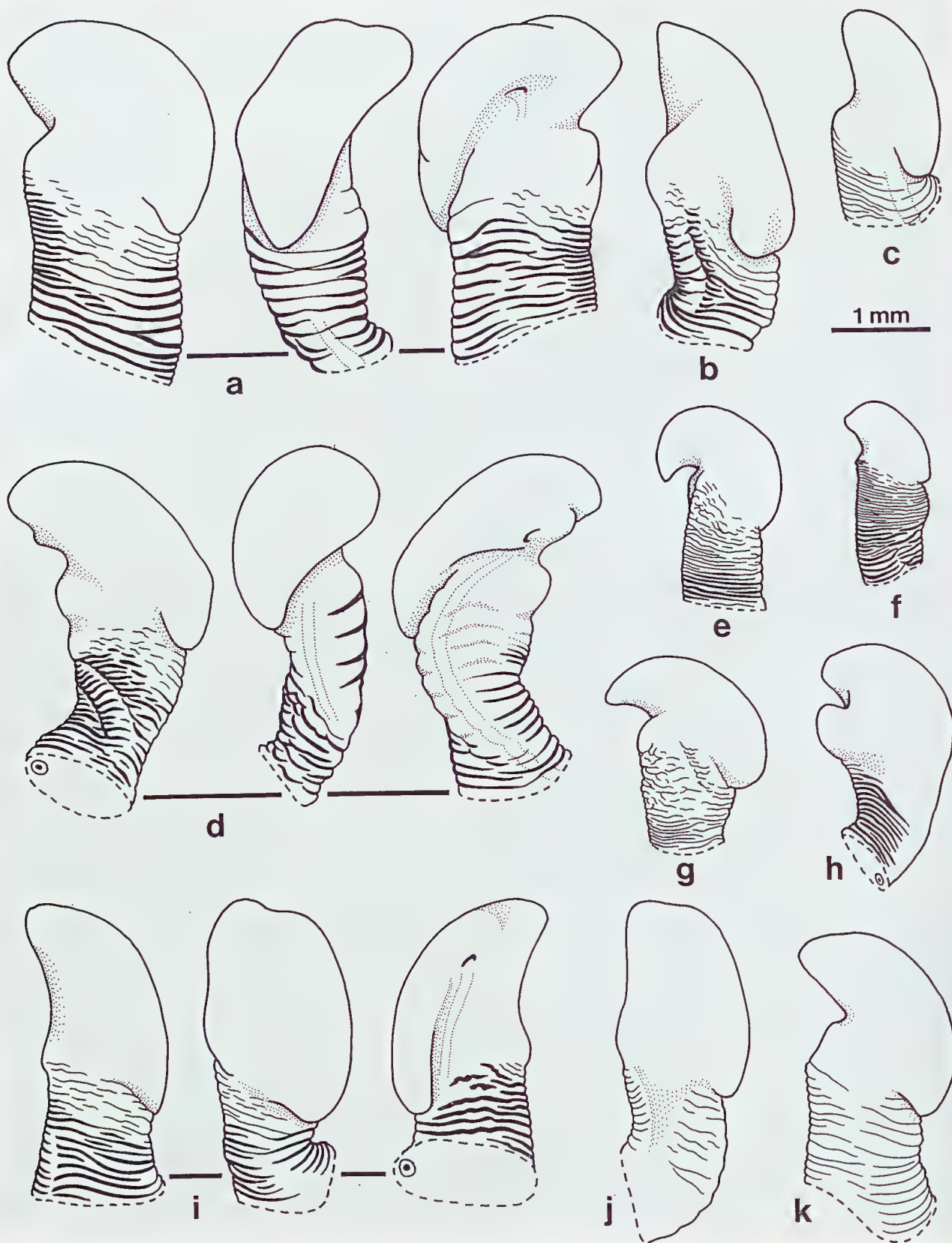


Fig.18. Penes of *Bembicium auratum* (Quoy & Gaimard): a,d, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); b,i, Bateman's Bay, N.S.W. (AMS C144364); c, North Keppel Island, Qld (AMS C144367); e,f,g, Magnetic Island, Qld (BMNH); h, Corinella, Western Port Bay, Vic. (NMV F52210); j,k, Proserpine River, Wilson, Qld (AMS C144335); a,d,i, each show lateral, ventral and medial views (relative to orientation of head), all others are lateral views.

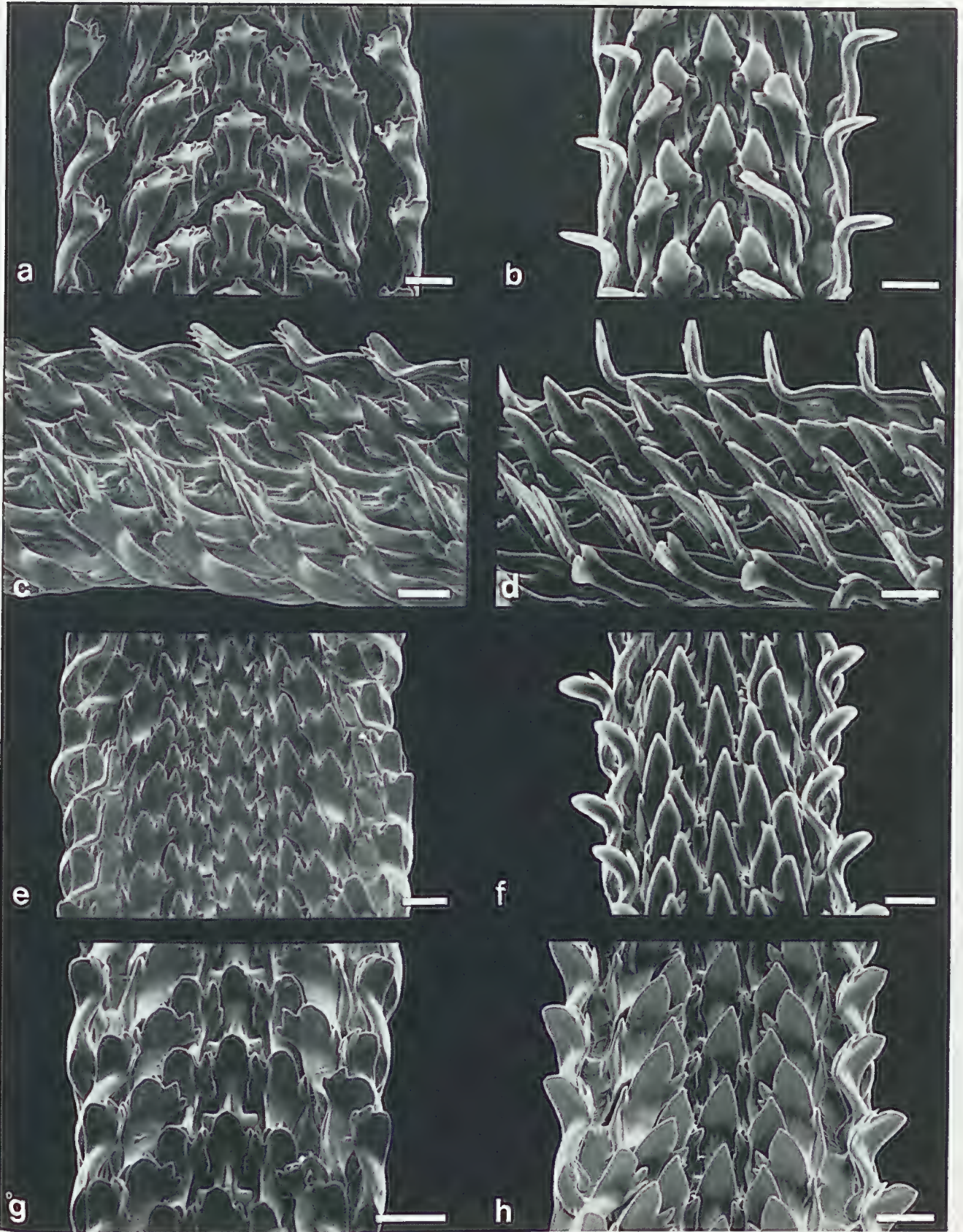


Fig.19. *Bembicium auratum* (Quoy & Gaimard) radulae: a,c,e (3 views), Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); b,d,f (3 views), Sidmouth, West Tamar River, Tas. (AMS C144332); g, Magnetic Island, Qld (BMNH); h, Minim Cove, Swan River estuary, W.A. (AMS C144325) (bars a-h = 50 µm).

sometimes hooked; base usually with black pigment.

PALLIAL OVIDUCT (Figs 3d, 4).

RADULA (Fig. 19). Length to 42 mm; relative length 1.98–2.66.

Distribution. **HABITAT.** Roots and trunks of mangroves, in estuaries and inlets; sometimes on sheltered rocky shores.

RANGE (Fig. 20). From Lizard Island, Queensland, south around the Australian coastline, including Tasmania, to Perth, Western Australia (also one specimen from Houtman Abrolhos Islands).

RECORDS. Queensland: Lizard Island (N; AMS); north of Cooktown (N; AMS); Low Isles (N; AMS); Missionary Bay, Hinchinbrook Island (N; DGR); Cockle Bay, Magnetic Island (N; DGR); Bowen (N; AMS); Lindeman Island (N; AMS); Hamilton Island (N; AMS); Shute Island, Shute Harbour (N; DGR); Brampton Island (N; AMS); Sarina (N; DGR, AMS); North Keppel Island (N; AMS); One Tree Island, Capricorn Group (S; AMS); Colleseum Inlet, south of Gladstone (N; AMS); Eurimbula Creek, south of Bustard Head (N; AMS); Burnett Heads (S; BMNH); Pinalba (S; AMS); Gatekeepers Bay, Hervey Bay (N;

AMS); Wathumba Creek estuary, Fraser Island (N; AMS); Tin Can Bay, north-east of Gympie (N; AMS); between Dunwich and Myora, Stradbroke Island (I; AMS, USNM); Goat Island, Moreton Bay (N; AMS); New South Wales: Brunswick Heads (S; AMS); Wooli (S; AMS); Nelson's Bay, Port Stephens (S; AMS); Lane Cove River (S; AMS); Kurnell (S; BMNH, USNM); Batemans Bay (S; DGR, AMS); Victoria: Mallacoota (S; AMS, NMV); Lakes Entrance (S; NMV); Corinella, Western Port Bay (S; NMV); Williamstown (S; NMV); Moyse River estuary, Port Fairy (S; AMS); Tasmania: Northeast River, Flinders Island (S; TM); Prosser River estuary (S; TM); Eaglehawk Bay, south-east Norfolk Bay (S; AMS); Saltwater River (S; TM); Petchey's Bay, Huon (S; TM); Schooner Cove, Port Davey (S; TM); Black River estuary (S; TM); Forth River (S; TM); South Australia: Largs North Beach, 19 km north of Adelaide (S; AMS); Patawalonga Creek (S; SAM); Port Noarlunga estuary (S; SAM); Western Australia: Oyster Harbour, Albany (S; BMNH, AMS, WAM); Kalgan River (S; AMS, WAM); Bunbury (S; AMS, WAM, USNM); Swan River estuary (S; AMS, WAM); Woodmans Point (S; WAM); Pelsart Group,

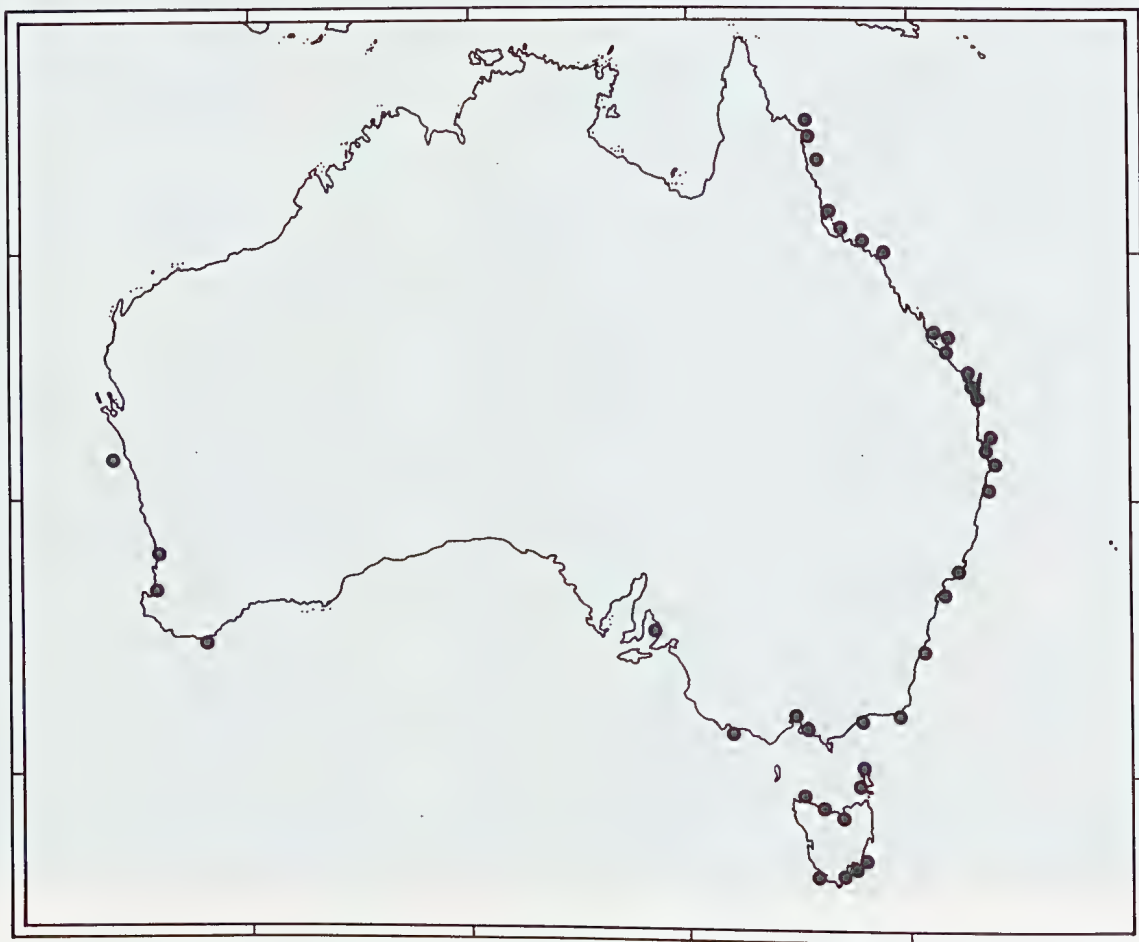


Fig. 20. Distribution of *Bembicium auratum* (Quoy & Gaimard).

Houtman Abrolhos Islands (S; WAM). Note: N, northern form; S, southern form; I, range of intermediates from N to S.

Remarks. The typical southern form of this species (Fig. 16c,h,j–m), occurring in southern Queensland and south and westwards around the coastline to the Houtman Abrolhos Islands, is easily distinguished from other members of the genus by its relatively tall spire, coarsely nodulose periphery (the nodules often black in eroded shells), and more numerous grooves above the periphery of the last whorl (seven to 11). In northern Queensland the form of the shell is different (Fig. 16a,b,d–g,i); the spire is lower, the periphery strongly keeled, the radial folds or nodules become obsolete on the last one to three whorls, and the aperture usually lacks black colour (as may the exterior of the shell also). For the present, these two forms are regarded as conspecific, since no consistent differences in penial or radular morphology could be detected, and in addition intermediate shells occur where the distributions of the two forms overlap. Genetic analysis of isoenzyme frequencies could well be used to examine the degree of similarity between northern and southern forms.

The detailed distribution of the two shell forms is interesting (see list of records above). The typical southern form is recorded as far north as Hervey Bay (25°S) and One Tree Island in the Capricorn Group (23°30'S), while the northern form is also found in Hervey Bay, and at Tin Can Bay (26°S) and Goat Island, Moreton Bay (27°S). A range of shell types, including northern, southern and intermediate shells, occurs in samples from Stradbroke Island (27°S), and also in a lot labelled 'Point Curtis' (AMS: probably = Port Curtis, 24°S). This pattern of distribution corresponds with the biogeographical boundary at 25°S and the northern affinities of Moreton Bay (Endean *et al.*, 1956a), and could be explained either by a direct ecophenotypic effect of temperature on shell form, or by the existence of geographical subspecies with different physiological tolerances and limited interbreeding in the zone of overlap.

A further aspect of variation in *Bembicium auratum* concerns the presence of dwarf populations of the northern form on offshore islands (Fig. 16d,e). Maximum adult sizes ranged from 6.7 to 11.9 mm in shell diameter in seven collections from islands north of 21°S (Lizard Island, Low Isles, Shute Island, Hamilton Island, Lindeman Island, Brampton Island, Goat Island), which may be compared with a range of 13.3 to 19.3 mm at eight mainland sites in the same region. Specimens from the large continental islands with turbid water and well-developed mangrove forests attained sizes in the same range as mainland shells (Hinchinbrook Island, 14.5 mm; Magnetic Island, 17.3 mm). A single shell from Hook Island (AMS) did not fit this pattern, measuring 17.6 mm in diameter. No preserved material of the dwarf forms was available for

comparison with mainland samples, but shell form was similar. It has been noted that the narrow mangrove fringes of small islands with clear water off the Queensland coast support assemblages of *Littoraria* species which differ from those in turbid, continental localities (Reid, 1986).

Bembicium nanum (Lamarck, 1822)

Figs 3c, 15i–p, 21–23

Trochus nanus Lamarck, 1822: 30 [9 syntypes, MHNG 1096/15, photograph of one seen; seas of New Holland].—Quoy & Gaimard, 1834: 273–274, pl. 62, figs 5–7; Delessert, 1841: pl. 36, figs 3 a–c; Deshayes & Milne Edwards, 1843: 150.

Bembicium nanum.—Philippi, 1846: 131–132; May, 1921: 48; May, 1923: pl. 22, fig. 21; Cotton & Godfrey, 1938: 10; MacPherson & Chapple, 1951: 118; Dakin, 1953, 1960: 247–248, pl. 61, fig. 7; Kershaw, 1955: 307; H. Anderson, 1958: 558–560, pls 3–5 d–f; D.T. Anderson, 1961 (development); MacPherson & Gabriel, 1962: 89, fig. 117; Bedford, 1965 (reproductive anatomy); Bedford, 1966 (oogenesis, embryology); Fretter, 1982: fig. 1 (anatomy); Ludbrook, 1984: 70, fig. 20i, pl. 11.

Risella nana.—Philippi, 1853: 6–7, pl. 1, figs 13–16; Chenu, 1859: 302, fig. 2125; Crosse, 1864: 234–236; Angas, 1867: 209; Smith, 1884: 61–62; Nevill, 1885: 159; Verco, 1908: 8.

Trochus acuminatus Wood, 1828: 16, pl. 5, *Trochus* fig. 6 [type not in BMNH; S. Sea].

Trochus planus Quoy & Gaimard, 1834: 274–275, pl. 62, figs 13, 14 [types lost (P. Bouchet, pers. comm.)], lectotype pl. 62, fig. 14; East Passage, Port-Western, Bass Strait [Western Port Bay, Victoria]; not Gmelin, 1791].

Bembicium planum.—Philippi, 1846: 131; Cotton & Godfrey, 1938: 10; MacPherson & Chapple, 1951: 118.

Risella plana.—Philippi, 1853: 5, pl. 1, figs 6, 7; Crosse, 1864: 236–237, pl. 11, fig. 2; Angas, 1865: 173; Angas, 1867: 209; Nevill, 1885: 158; Verco, 1908: 8.

Littorina australis Gray, 1839: 141 [lectotype BMNH 1968365, 21.7 x 17.4 mm, one of 2 paralectotypes is probably *B. vittatum*; New Holland; not Gray, 1826, see Rosewater, 1970: 487].

Bembicium pictum Philippi, 1846: 132 [lectotype Philippi, 1853: pl. 1, fig. 11; Vandiemensland [Tasmania]].

Risella picta.—Philippi, 1853: 6, pl. 1, figs 11, 12.

Risella grisea Philippi, 1851: 31–32 [no locality].—Philippi, 1853: 8, pl. 1, figs 19, 20 [lectotype fig. 19].

Risella crassa Dunker, 1861: 42 [lectotype ZMB 19.4 x 15.5 mm; Sydney].

Risella aurata.—Tenison-Woods, 1877 [in part, not Quoy & Gaimard, 1834].

Littorina melanostoma.—Tenison-Woods, 1879: 61–65 [in part, not Gmelin, 1791].

Risella melanostoma.—Tryon, 1887: 262–263, pl. 49, figs 99, 10–14, 16–19 [in part, not Gmelin, 1791]; Pritchard & Gatliff, 1902: 92–94 [in part, not Gmelin, 1791]; Kesteven, 1903: 623–631, pl. 30, figs 1–13 (anatomy) [not Gmelin, 1791].

Bembicium melanostoma.—May, 1921: 48 [in part, not Gmelin, 1791]; Musgrave, 1929: 344 [not Gmelin, 1791]; Iredale, 1931: 208–209 [not Gmelin, 1791]; Allan, 1950: 80–81, fig. 19, no. 4 [not Gmelin, 1791];

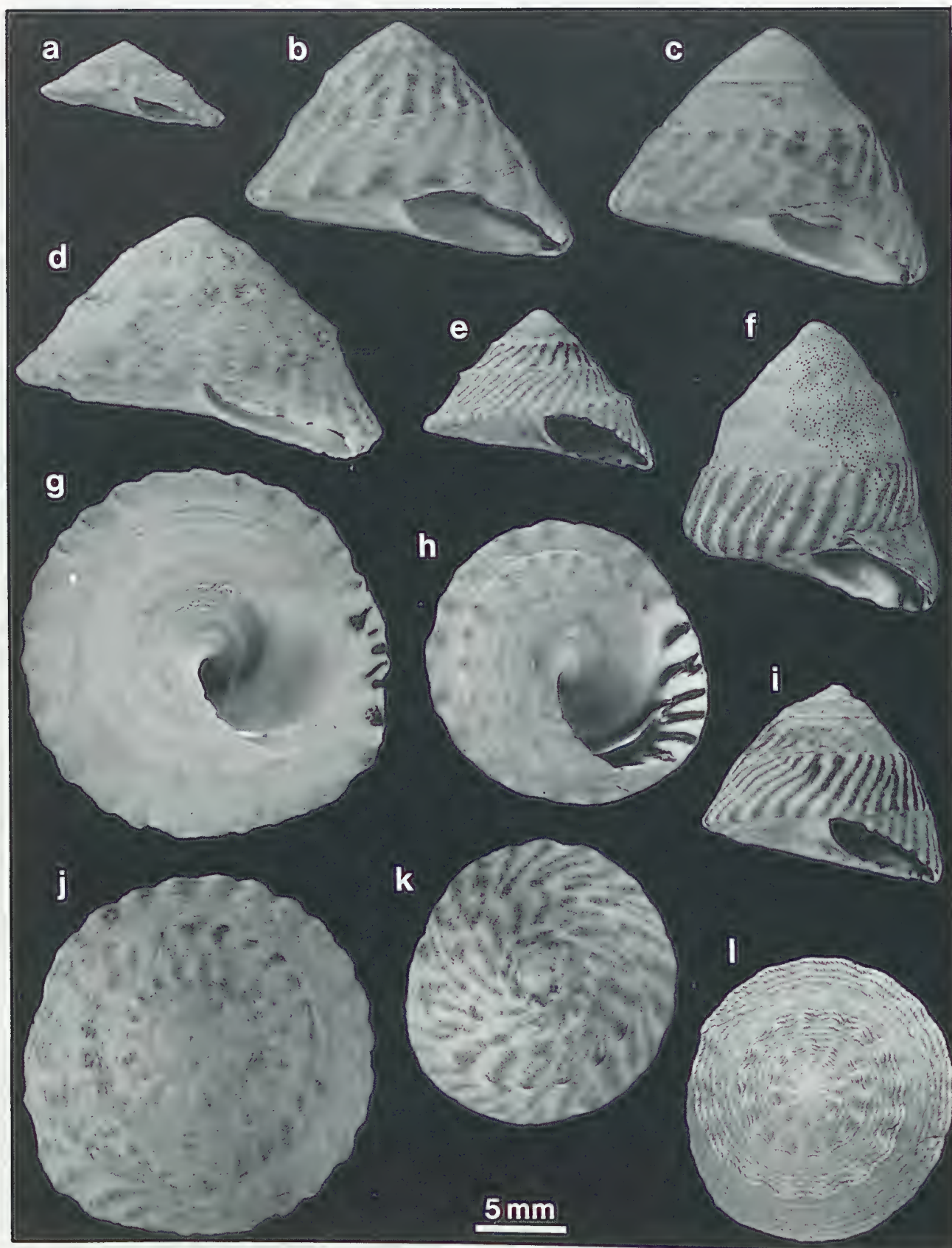


Fig.21. *Bembicium nanum* (Lamarck): a, juvenile, Normanville, S.A. (AMS); b, Honeymoon Beach, Jervis Bay, N.S.W. (AMS C144329); c, Charlesworth Bay, Coffs Harbour, N.S.W. (AMS C144327); d,g,j (3 views), Normanville, S.A. (AMS); e,i, Tomahawk Island, north-east Tas. (AMS C144287); f, Stony Point, Western Port Bay, Vic. (BMNH); h,k (2 views), Whisky Bay, Wilson's Promontory, Vic. (AMS C144399); l, whitened to show sculpture, Alexandra Headland, Qld (BMNH).

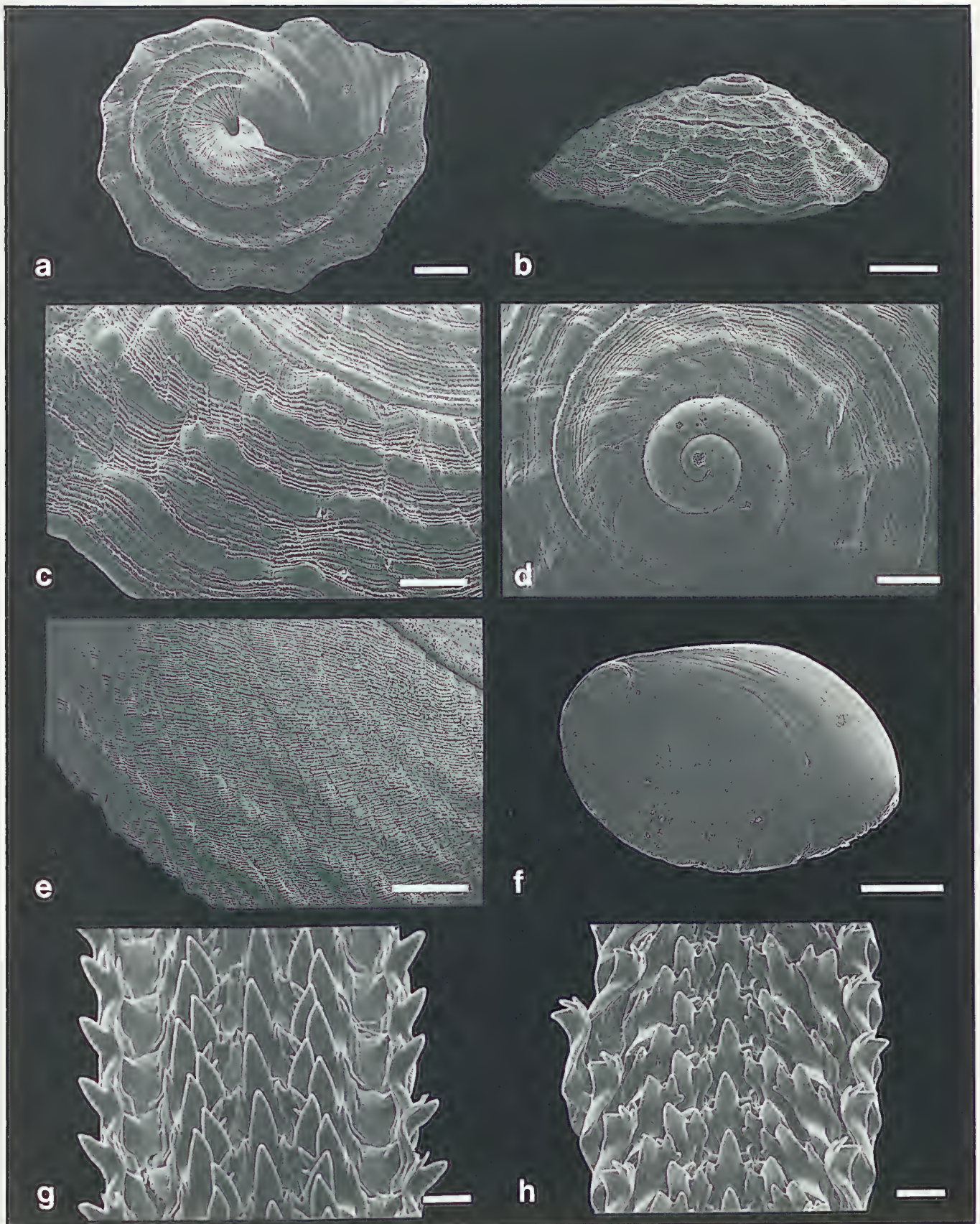


Fig.22. *Bembicium nanum* (Lamarck): a,b-d (3 views), juveniles, Iluka, N.S.W. (AMS C144387) (bars a,b = 500 μ m; bars c,d = 200 μ m); e, Point Hastings, Murwillumbah, N.S.W. (AMS C144323) (bar = 1 mm); f, operculum, Tomahawk Island, Tas. (AMS C144287) (bar = 1 mm); g, radula, Flinders, Vic (AMS C144314); h, radula, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288) (bars g,h = 50 μ m).

Iredale & McMichael, 1962: 39 [in part, not Gmelin, 1791].

Nomenclature. The distinctively striped exterior and apertural margin leave no doubt as to the identification of *Trochus acuminatus* Wood, *Trochus planus* Quoy & Gaimard, *Bembicium pictum* Philippi and *Risella grisea* Philippi, although all are represented only by figures. *Littorina australis* Gray, 1839 is a primary homonym of a species published by the same author in 1826; the latter is now placed in the genus *Nodilittorina* (Rosewater, 1970). Examination of the types of *Risella crassa* Dunker showed this species to be synonymous with *B. nanum*, and not with 'Queensland specimens classified as *B. melanostoma*' (= *B. auratum*) as suggested by H. Anderson (1958). The marked allometry exhibited by this species (Fig. 1) led to the identification of flattened juveniles (Fig. 21a) as *planus* Quoy & Gaimard by many authors.

Shell. (Fig. 21). **DIMENSIONS.** Adult size range 10–25 mm diameter; mean height/diameter ratio 0.798 (st. dev.=0.135, range 0.488–1.473, n=100 from 56 localities).

SHAPE. Teleoconch 5.5–7 whorls; spire commonly severely eroded; shell thick. Outline low to equilaterally conical; sides lightly convex, base flat. Periphery strongly keeled, sometimes conspicuously flanged; sutures usually indistinct, but well marked if preceding whorl flanged. Small umbilicus in juvenile shells, becoming closed during third whorl. Within aperture a thickened ridge becomes prominent below peripheral keel in adult shells.

SCULPTURE. (Fig. 22a–e). Protoconch smooth, 0.39 mm diameter, 1.25–1.5 whorls, terminated by inconspicuous sinusigera ridge. First whorl of teleoconch marked by faint spiral striae and growth lines. On second whorl 4–5 wide primary spiral grooves appear above periphery, 1–2 times width of the irregularly rounded or nodulose ribs between them; grooves contain microsculpture of sharp spiral threads; also on second whorl 13–15 radial folds appear, stretching from suture to sharply flanged periphery. On subsequent whorls spiral grooves increase to 7–9, separated by ribs which are made beaded or even minutely lamellose by radial growth lines. Microsculpture spreads over ribs as well as



Fig.23. Distribution of *Bembicium nanum* (Lamarck).

grooves, becoming progressively more oblique in relation to spiral ribs, but remaining perpendicular to apertural margin. Radial folds increase to 15–20 per whorl, most prominent at periphery, but usually become obsolete on last 1–2 whorls. Spiral ribs become obsolete on last whorl, leaving surface smooth to the eye, sculptured only by oblique, irregular, but closely spaced, growth lines and fine, sharp, microsculptural threads perpendicular to the growth lines. Since shells are commonly severely eroded, with only last whorl relatively undamaged, radial and spiral sculpture of juvenile shell is only visible in small individuals or in those from sheltered habitats. On early whorls peripheral keel is marked by a strong flange, thrown into undulations by the radial folds on the upper surface. On juvenile shells of 2–3 whorls base is marked by 3 sharp spiral ridges, of which outermost is most prominent. On whorl 4 a fourth ridge appears between outer 2, and these 4 remain prominent on succeeding whorls. The flat grooves between are 2–4 times ridge width, marked by fine, closely spaced growth lines and faint spiral microsculpture; one additional riblet may be interpolated between outer 2 ridges on base of final whorl, and 2 more between outer ridge and peripheral keel.

COLOUR. Shell white, cream or pale yellow; on first 4–5 whorls keel and radial folds remain pale, spaces between grey to purple brown. Dark colour becomes restricted to radial folds; last two whorls marked by oblique black or purple brown lines, which tend to bifurcate towards periphery; dark lines number 18–38 at periphery of last whorl; striped pattern sometimes more diffuse. Base pale, with sparse dark spots on ridges. Columella white, cream, or pale salmon orange. Apertural margin white, conspicuously marked by 4–10 black or brown stripes corresponding to outer colour pattern; callus within aperture, on outer wall, dark brown or cream; base of aperture pale.

Animal. PENIS (Fig. 15i–p). Filament very small, no more than a rounded papilla on the wrinkled base.

PALLIAL OVIDUCT (Fig. 3c).

RADULA (Fig. 22g, h). Length to 48 mm; relative length 2.31–2.95.

Distribution. HABITAT. Upper eulittoral of moderately exposed rocky shores.

RANGE (Fig. 23). From Yeppoon, Queensland, south around the Australian coastline, including Tasmania, to Port Lincoln, South Australia (possibly further westwards, since few collections have been made from the Great Australian Bight).

RECORDS. Queensland: Yeppoon (AMS); Facing Island (AMS); Port Curtis (AMS); Burnett River mouth (AMS); Hervey Bay (AMS); Noosa Heads (AMS); Mooloolaba (AMS); Point Lookout, Stradbroke Island (AMS, USNM); New South Wales: Point Hastings, east of Murwillumbah (AMS); Iluka Bluff (AMS); Coffs Harbour (AMS); Nelson's Bay,

Port Stephens (AMS); Collaroy (AMS, USNM); North Harbour, Sydney (DGR); Jervis Bay (AMS); Batemans Bay (AMS); Merimbula (AMS); Victoria: Mallacoota (AMS); Wingan Inlet (NMV); Cape Conran (NMV); Whisky Bay, Wilson's Promontory (AMS); Cat Bay, Phillip Island (NMV); Flinders (AMS); Moonlight Head, Otways (NMV); Point Danger, Portland Bay (NMV); Tasmania: Palana, Flinders Island (TM); Eddystone (TM); Swansea, Great Oyster Bay (AMS); Pirates Bay, Eaglehawk Neck (AMS); Simpsons Bay, Bruni Island (TM); Trial Harbour (TM); Green Point, Marrawah (TM); Hunter Island (TM); King Island (TM); South Australia: Beachport (AMS); Robe (SAM); Victor Harbour (AMS); Second Valley (SAM); 2 miles south of Normanville (AMS); Blanche Point, north of Aldinga (AMS); Glenelg (SAM); Redbank, Nepean Bay, Kangaroo Island (AMS); Vivonne Bay, Kangaroo Island (AMS); Corny Point (AMS, USNM); Port Augusta (AMS); Port Lincoln (SAM).

Remarks. This species is the most easily recognised in the genus, characterised by a depressed and sharply keeled outline, three to four strong ribs on the base of juveniles (which remain the most prominent on the adult shell), and the colour pattern of oblique black stripes, also visible at the edge of the apertural lip. One geographical form can be recognised; in St Vincent and Spencer's Gulfs and on Kangaroo Island, South Australia, some collections are of unusually large shells with strongly flanged, crenulated margins, in which the typical striped pattern is diffuse or almost absent (Fig. 21d,g,j). Typical examples occur in the same geographical range, however, and no anatomical or radular differences between the two forms could be detected.

Bembicium altum (Tate, 1894)

Fig. 24b

Risella alta Tate, 1894: 184, pl. 11, fig. 4 [holotype SAM T240; Spring Creek and Muddy Creek [Victoria], 'Eocene' ['Spring Creek' refers to Jan Juc Formation at Torquay, Janjukian Stage, late Oligocene to early Miocene; 'Muddy Creek' refers to Muddy Creek Formation at Clifton Bank, Muddy Creek, Balcombian Stage, Middle Miocene; both localities Darragh, 1985: 101–104 and pers. comm.]].

Bembicium altum.—Darragh, 1970: 153.

Shell. (Fig. 24b). DIMENSIONS. Holotype diameter 6.4 mm, height 6.0 mm; 6 worn paratypes approximately 4 mm diameter; height/diameter ratio of holotype 0.94.

SHAPE. Teleoconch approximately 5 whorls. Outline equilaterally conical, sides straight; last 2 whorls slightly concave, earlier whorls bear nodules at shoulder; base flat. Periphery strongly keeled, sutures indistinct. Umbilicus closed.

SCULPTURE. 3–5 broad grooves above peripheral keel, separated by slightly nodular, rounded ribs. Radial sculpture consists of 11–16 short folds or

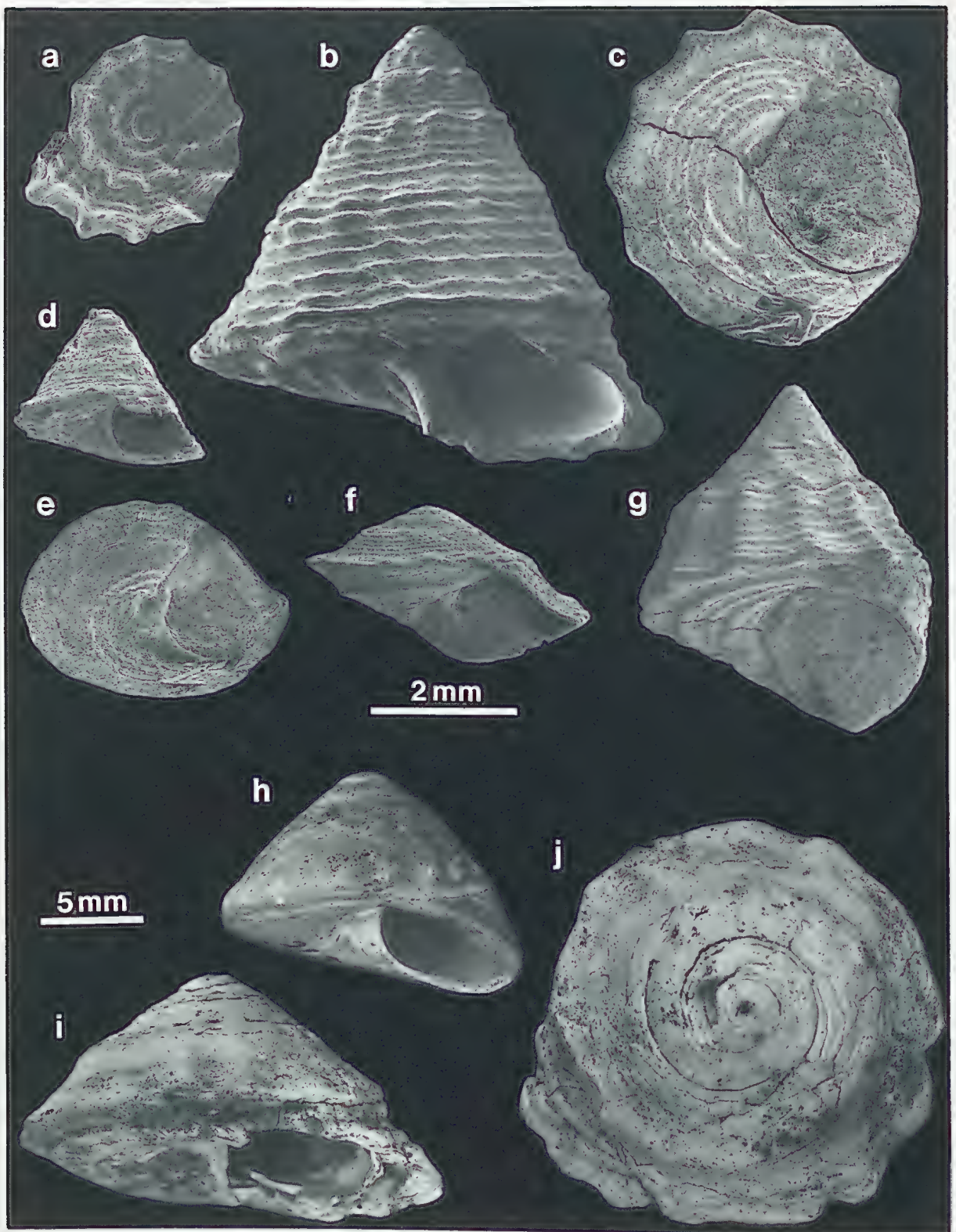


Fig. 24. Fossil *Bembicium* species: a, *Bembicium* sp., Pinehill Stream, Waimamaku Valley, Northland, New Zealand, Otaian Stage, Lower Miocene (NZGS TM6663); b, *B. altum* (Tate), holotype, 'Spring Creek and Muddy Creek', Vic., Late Oligocene to Middle Miocene (SAM T240); c, g (2 views), *B. priscum* Powell & Bartrum, holotype, Oneroa, Waiheke Island, New Zealand, Otaian Stage, Lower Miocene (Geol. Dept., Auckland Univ. G5535); d, *B. priscum*, *B. discoideum* n. sp., holotype, Pinehill Stream, Waimamaku Valley, Northland, New Zealand, Otaian Stage, Lower Miocene (NZGS TM6665); e, f (2 views), *B. 'melanostoma' group*, Rangitikei River, Manawatu, New Zealand, Castlecliffian, Pleistocene (NZGS TM6661); i, j (2 views), *Bembicium* sp., Thomas River, Castle Hill Basin, Canterbury, New Zealand, Altonian Stage, Lower Miocene (NZGS TM6662).

nodules at suture of early whorls, becoming obsolete on last 2 whorls. In smaller specimens, peripheral keel bears about 13 slightly upturned, blunt nodules, which crenulate the margin, but crenulations are weak and irregular on largest shell. Base with 3 strong ribs in smaller specimens; base of holotype with 4 strong ribs and 2 threads in outermost groove.

Distribution. The localities given by Tate (1894) are of late Oligocene to Middle Miocene age (see above). In addition to the type collection in SAM, two specimens from Spring Creek are present in NMV (not seen; T. Darragh, pers. comm.).

Remarks. The low number of grooves above the periphery and of ridges on the base, and the prominent shoulder nodules on early whorls are distinguishing features of this species.

***Bembicium priscum* Powell & Bartrum, 1929**

Fig. 24c,d,g

Bembicium priscum Powell & Bartrum, 1929: 414, figs 7, 8 [holotype Geology Dept., Auckland Univ. G5535, 2 paratypes G5536–7; Oneroa, Waiheke Island, New Zealand, 'Hutchinsonian Stage, Upper Oligocene' [Cape Rodney Formation, north-west end of Oneroa Beach, Waiheke Island, Auckland, Otaian Stage, Lower Miocene; J.A. Grant-Mackie, pers. comm.]].—Fleming, 1966: 42.

Shell. (Fig. 24c,g,d). **DIMENSIONS.** Holotype diameter 3.8 mm, height 4.5 mm; height/diameter ratio 1.18.

SHAPE. Teleoconch approximately 5 whorls. Outline onion-shaped, at first concave, convex at last whorl; sides of early whorls straight, last 2 whorls concave, final $\frac{1}{4}$ whorl becoming convex; base flat, becoming convex. Periphery at first strongly flanged, becoming rounded at end of last whorl; sutures slightly impressed. Umbilicus closed.

SCULPTURE. Six grooves above peripheral keel, separated by rounded ribs approximately equal to groove width. Strong radial sculpture of 12 folds per whorl, from suture to periphery, aligned on succeeding whorls; folds crenulate the margin, but become obsolete just behind apertural lip. Base with 4 ribs, and a single thread in each of 2 outer grooves.

Distribution. **RANGE AND AGE.** Known from 3 collections, widely scattered in New Zealand: in Auckland, Hawke's Bay and Southland; basal Miocene to early Upper Miocene.

RECORDS. New Zealand: Cape Rodney Formation, north-west end Oneroa Beach, Waiheke Island, Auckland (NZ fossil record no. R10/f9001), Otaian Stage, Lower Miocene (Geol. Dept., Auckland Univ.); conglomerate, 1.6 km up Tutaematua Stream, Nuhaka, Wairoa district, Hawke's Bay (X19/f7499, NZGS loc. no. GS 1517), Lillburnian or Waiauian Stage, late Middle to early Upper Miocene (NZGS); west bank Maitua River, 2.2 kms east of Brydone, 7.2 kms downstream from

Maitua Bridge, near Gore, Southland (F46/f8492, GS 3600), Waitakian Stage, basal Miocene (NZGS).

Remarks. The above description is based on the type collection, and the onion shape and rounded last part of the final whorl, without radial folds, seem distinctive. The second collection listed above is a single poorly preserved shell with broken spire, but agrees with the holotype in other characters.

The third collection is doubtfully referable to *B. priscum*, comprising 27 specimens all less than 3 mm in diameter, of which only one (Fig. 24d) is well preserved. All are approximately equilaterally conical in outline, with straight sides, four to five basal ridges and six to eight grooves above the strong peripheral keel, which bears 12 to 13 pointed crenulations which are not continued as radial folds above the periphery. The umbilicus is open in the smallest specimens. The shape and sculpture are similar to the early whorls of *B. priscum*, except that no radial folds are present, but this feature is variable in Recent species. One specimen shows slight rounding of the last whorl, as in *B. priscum*.

***Bembicium discoideum* n. sp.**

Fig. 24e,f

Type material. **HOLOTYPE** NZGS TM 6665, 8 **PARATYPES** NZGS 6666–73, Pinchill Stream, near waterfall 200 m up from road, Waimamaku Valley, south of Hokianga Harbour, Northland, New Zealand (N.Z. fossil record no. O6/f40, NZGS loc. no. GS 12601), Otaian Stage, Lower Miocene.

Etymology. Greek, disc-like.

Shell. (Fig. 24e,f). **DIMENSIONS.** Shell size range 1.2–4.0 mm diameter; mean height/diameter ratio 0.578 (st. dev.=0.040, range 0.517–0.632, n=9, from type locality).

SHAPE. Teleoconch approximately 3–3.5 whorls; shell solid. Spire depressed, sides almost straight; base convex. Periphery bears strong, slightly upturned flange, at approximately half total shell height. Last whorl concave above periphery. Sutures indistinct. Small, open umbilicus. Columella thickened and angled at base.

SCULPTURE. Protoconch smooth, low, approximately 0.3 mm diameter and 1.25 whorls, no sinusigera ridge preserved. Teleoconch sculptured by 6–8 equally spaced spiral grooves above periphery. Margin with slight radial folds, producing 12–17 slight crenulations of the peripheral flange. On whorl 3 base has 3 spiral ribs, outermost the strongest, innermost being margin of umbilicus; number of ribs increases to 5–6, outermost remaining strongest; 3–5 spiral threads develop between strongest rib and periphery.

Distribution. **RANGE AND AGE.** Only known from 2 localities in the vicinity of Hokianga Harbour, Northland, New Zealand, from the Otaian Stage of the Lower Miocene (A.G. Beu, pers. comm.).

RECORDS. New Zealand: type locality (see above); blue-grey siltstone with thin shelly lenses, road cutting on north side of Otueka Hill, road to Mitimiti, north shore Hokianga Harbour, Northland (O5/f21, GS 12600) (NZGS).

Remarks. Despite small size, the holotype appears to be a mature specimen, shown by the delimitation of the parietal area of the aperture, which suggests an interruption to growth. The species is more depressed than any other *Bembicium*, and the base more convex. In addition, the open umbilicus is unusual, and the flange or 'lip' at the base of the columella is unique.

The second collection listed above is of a single specimen, of globular shape, with a rounded final whorl. The first two and one half whorls are as in the type collection, and the peculiar shape of the last whorl appears to be the result of damage during growth. It should, however, be noted that in *B. priscum* the last whorl does become rounded, giving the shell a globular shape.

Fossil *Bembicium* spp. indet.

A single specimen from the New Zealand Altonian Stage, Lower Miocene (Fig. 24i,j, NZGS TM6662, north bank of Thomas River, 400 m upstream from junction with Porter River, Castle Hill Basin, Canterbury, upper muddy beds, N.Z. fossil record no. K34/f9511, NZGS loc. no. GS 4681) is too poorly preserved for description, but is reminiscent of *Bembicium nanum* in outline. There are traces of four grooves above the periphery just behind the apertural lip, too few for *B. nanum*.

Two apparently juvenile specimens (Fig. 24a) were present with the type collection of *B. discoideum* (NZGS TM6663-4) from the Otaian Stage of the Lower Miocene. These measure 2.9 and 2.4 mm in diameter (height/diameter ratios 2.23, 2.0), with six grooves above the crenulated periphery, 12 strong radial folds, and are similar to juveniles of *B. nanum*. The base bears about five ridges, of which the outermost is strongest, and the umbilicus is rather wide, which are points of difference from *B. nanum*.

The occurrence of *Bembicium* aff. *melanostoma* in the Pleistocene of New Zealand has been discussed (Fig. 24h).

Genus *Risellopsis* Kesteven, 1902

Risellopsis Kesteven, 1902: 319-320 [type species by original designation *Fossarina varia* (Hutton) [i.e. *Adeorbis varius* Hutton]; not *Risellopsis* Cossmann, 1908, renamed *Riselloidea* Cossmann, 1909].

Diagnosis. As for the only known species, *R. varia*. Shell depressed trochoidal, periphery keeled or rounded, base convex, umbilicus open. Teleoconch sculptured by spiral ribs, 0-3 above peripheral keel, 4 on base. Periostracum produced into bristles on spiral ribs. Operculum paucispiral type B.

Gonochoristic. Prostate and anterior vas deferens both open grooves, open penial sperm groove; penis simple, small non-glandular lobe on ventral edge of base, opening of sperm groove almost terminal, minute papilla at filament tip, subepithelial glands absent. Pallial oviduct comprises single proximal spiral of albumen gland, and enlarged distal jelly gland, the latter divided into inner and outer chambers capsule glands absent; opening to mantle cavity small and subterminal; posterior seminal receptacle joined to pallial oviduct by long duct opening just anterior to opening of pallial oviduct to mantle cavity; renal oviduct joins albumen gland posteriorly; anterior bursa copulatrix. Benthic gelatinous egg masses; development planktotrophic. Radula littorinoid; main cusp of rachidian tooth somewhat reduced; main cusp on each lateral and inner marginal tooth bluntly truncated. Salivary glands anterior to nerve ring around oesophagus.

Risellopsis varia (Hutton, 1873)

Figs 5, 25-27

Adeorbis varius Hutton, 1873: 35 [lectotype NMNZ M160, paratype M1822; Stewart's Island; Chatham Islands].

Risella (?) *varia*.—Hutton, 1878: 27.

Fossarina varius.—Hutton, 1880: 79; Hutton, 1882: 164.

Risellopsis varia.—Kesteven, 1902: 320-321, fig. 29 (radula, operculum), figs 30-32; Suter, 1913: 191-192, pl. 35, fig. 13; Odhner, 1924: 21; Finlay, 1928: 241; Powell, 1937: 67, pl. 9, fig. 11; Fleming, 1966: 42; Morton & Miller, 1968: 80, 353, figs 23, 77; Pilkington, 1974: 411-413, fig. 1 (egg masses, veligers); Pilkington, 1976: 338, fig. 1a-c (veligers); Powell, 1979: 88-89, fig. 13, no. 7.

Risellopsis varia var. *carinata* Kesteven, 1902: 321-322, figs 33-35 [holotype AMS C11422; New Zealand].—Suter, 1913: 192, pl. 35, fig. 14; Bucknill, 1924: 38, pl. 6, figs 21, 21a; Finlay, 1928: 241.

Nomenclature. The development of the spiral ribs at and above the periphery is variable, and *R. varia* var. *carinata* is simply a strongly sculptured form of this species.

Shell. (Fig. 25). **DIMENSIONS.** Shell size range 3.1-8.3 mm diameter; mean height/diameter ratio 0.671 (st. dev.=0.079, range 0.500-0.860, n=42, from 23 localities).

SHAPE. Teleoconch approximately 3.5-5 whorls; apical whorls commonly eroded; shell solid. Spire low; whorls rounded or shouldered; base convex. Periphery usually bears a strong rib or keel, but is more uniformly rounded in shells with weak sculpture; sutures impressed. Small, open umbilicus, sometimes partly covered by inner lip of aperture. Inner margin of aperture uniformly rounded.

SCULPTURE. (Fig. 26a). Protoconch not seen. Teleoconch whorls sculptured by spiral ribs, of which strongest is that at periphery, which is



Fig. 25. *Risellopsis varia* (Hutton): a, Sumner, New Zealand (BMNH); b, Portobello, Otago Harbour, N.Z. (NMNZ M16553); c,e, Ringaringa, Stewart Island, N.Z. (NMNZ M19595); d, Kapo Wairua, N.Z. (NMNZ M59386); f, Titirangi Bay, Marlborough Sounds, N.Z. (NMNZ M40667); g,h, Marakopa, Kawhia, N.Z. (NMNZ M18796); i,j, Karaka Bay, Cook Strait, N.Z. (NMNZ M2412).

usually developed as a carina; in addition, a rib or carina usually present on shoulder, a smaller rib towards suture; in the most strongly sculptured shells a third dorsal rib may appear at suture, rarely these three may be nodular or beaded. Microsculpture consists of fine spiral striae between ribs, and fine radial growth lines. Base sculptured by 4 equidistant spiral ribs (excluding peripheral keel), becoming weaker towards centre; innermost rib outlines umbilicus. In well preserved shells periostracum produced into row of bristles on each spiral rib; bristles most obvious on base, where they reach 0.2 mm in length.

COLOUR. Shell cream to horn colour; pattern of irregular brown blotches which extend from suture to shoulder (or periphery), numbering 6–8 (rarely 4) on last whorl; 2 continuous brown spiral lines, 1 on each side of shoulder rib, which is itself usually pale but sometimes brown; sometimes third brown line nearer suture. Base pale brown, lighter at periphery; umbilicus cream. Aperture cream, brown exterior pattern showing through, dorsal side of aperture often brown; columella white.

Animal. HEAD (Fig. 27e).

PENIS (Fig. 27a–d). No clear division between wrinkled base and smooth distal filament; blunt,

with minute terminal papilla; open sperm groove, terminating a little before the tip; small non-glandular lobe protrudes from dorsal side of base.

PALLIAL OVIDUCT (Fig. 5).

RADULA (Fig. 26c,d). Length to 11 mm; relative length 1.15–1.94.

Distribution. HABITAT. Upper eulittoral of rocky shores, in crevices amongst barnacles and *Modiolus*.

RANGE (Fig. 9). Throughout New Zealand, including Stewart Island and Chatham Islands.

RECORDS. New Zealand: North Island: Kapo Wairua, Spirits Bay (NMNZ); Whangaroa Harbour (AIM); Tryphena, Great Barrier Island (AIM); Takapuna (BMNH, USNM); Otarawairere Bay, Ohope (NMNZ); Marakopa, Kawhia (NMNZ); Karaka Bay (NMNZ); South Island: Titirangi Bay, Marlborough Sounds (AMS, NMNZ); Fossil Point, North Nelson (NMNZ); Sumner (BMNH, USNM); Caroline Bay, Timaru (USNM); Hampden (USNM); Portobello, Otago Harbour (NMNZ); Riverton (AIM); Open Bay Islands (NMNZ); Stewart Island: Ringaringa (USNM, NMNZ); Thule, Paterson Inlet (AIM); Chatham Islands: Red Bluff (NMNZ); Waitangi (AIM); Wharekouri (USNM).

Remarks. This species is variable in shell

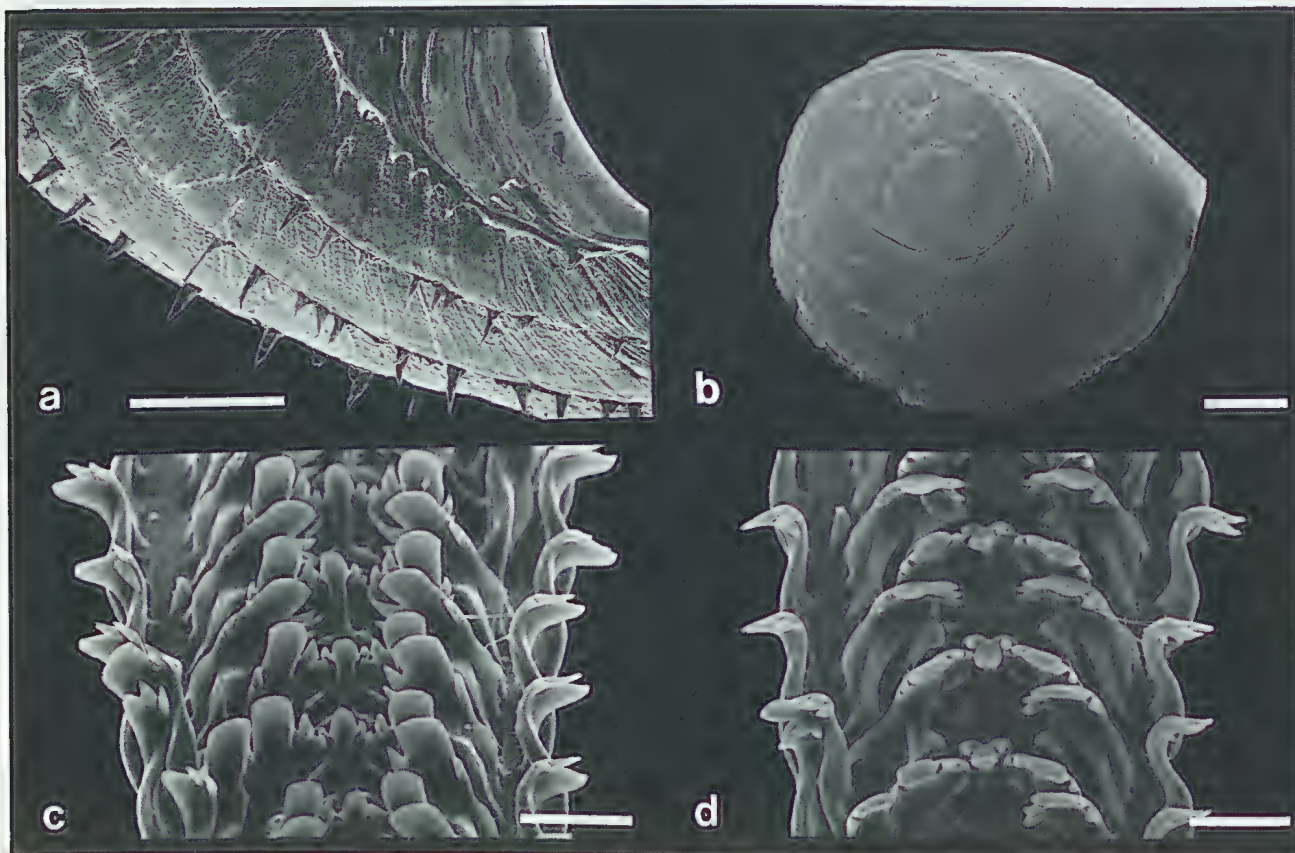


Fig. 26. *Risellopsis varia* (Hutton): a, periostracal bristles on base, Ringaringa, Stewart Island, New Zealand (NMNZ M19595) (bar = 500 μ m); b, operculum, Ringaringa, Stewart Island, N.Z. (NMNZ M80806) (bar = 500 μ m); c,d (2 views), radula, Ringaringa, Stewart Island, N.Z. (NMNZ M80806) (bar = 50 μ m).

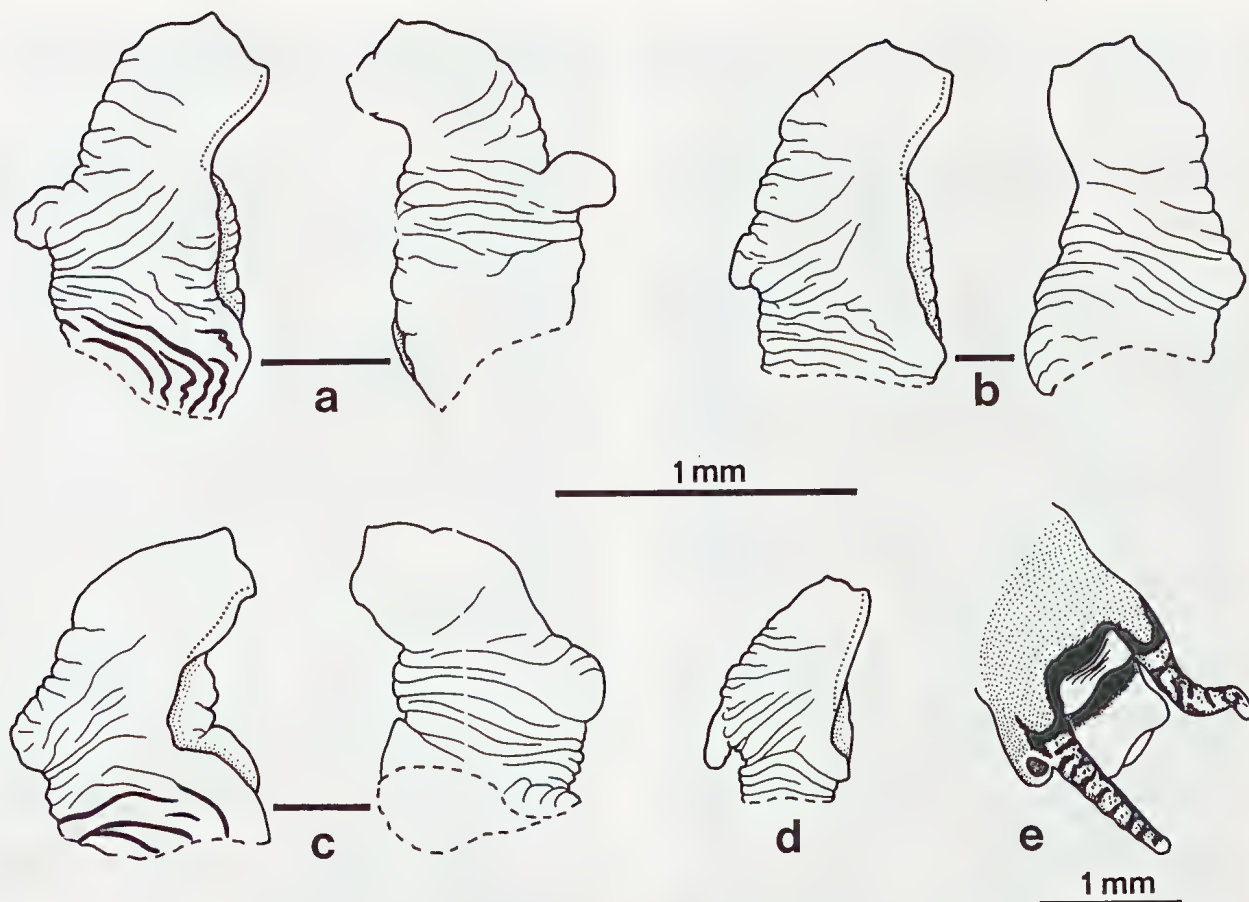


Fig. 27. *Risellopsis varia* (Hutton): a–d, penes; a–c, Ringaringa, Stewart Island, New Zealand (NMNZ M80806), lateral and medial views (relative to orientation of head); d, Titirangi Bay, Marlborough Sounds, N.Z. (AMS C144417), lateral view; e, head, Ringaringa, Stewart Island, N.Z. (NMNZ M80806).

sculpture, some specimens being almost smooth (Fig. 25h) while others are strongly carinate (Fig. 25a,c,f). As noted by Finlay (1928), gradations between these extremes are frequent and there is no apparent pattern of geographical variation in shell sculpture. The shape of the shell (especially of depressed forms, Fig. 25f) shows remarkable convergence with species of *Peasiella* (e.g. *P. isseli* (Semper in Issel)), which occupy a similar habitat in the tropical Indo-Pacific. The similarities with *P. isseli* extend to the presence of bristles on the periostracum, a feature rare in littorinids. One geographical trend which may be noted is that shells attain larger size in the south (Morton & Miller, 1968: 80). The maximum size of specimens seen from North Island was 5.8 mm in diameter, from South Island 7.1 mm, and from the Chatham Islands 8.3 mm.

A single Pleistocene fossil of *R. varia* is present in the NZGS (Brunswick marine sand member of Brunswick Formation, Mt. Jowett, Wanganui, N.Z. fossil record no. R22/f7416, NZGS loc. no. GS 4151; age: Terangian local stage of Hawera Series; late oxygen isotope stage 9 of Shackleton & Opdyke; A.G. Beu, pers. comm.).

Other fossils from New Zealand which have been classified as *Risellopsis* should be transferred to the Vitrinellidae.

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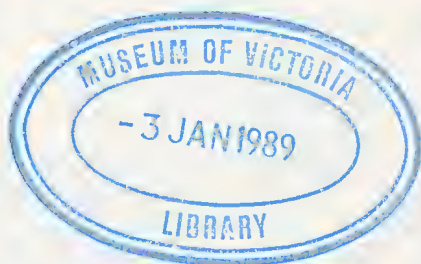
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Hermit Crabs from North Australian and Eastern Indonesian Waters (Crustacea Decapoda: Anomura: Paguroidea) Collected During the 1975 *Alpha Helix* Expedition

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ABSTRACT. Fifty-two species of hermit crabs of the families Coenobitidae, Diogenidae and Paguridae were collected in the Arafura Sea and in Maluku (Moluccas), Indonesia. Five of these species were previously unrecorded from the Arafura Sea and Torres Strait. At the Banda Islands, where the major part of the collecting was done, 34 out of 37 species are reported for the first time. The collection included 18 new records for Seram and 14 for Saparua. Four new species are described from Maluku. Live colour notes and information on natural history are presented for most of the species in the collection, and associations are noted with anemones, rhizocephalans, cirolanid and parasitic isopods, copepods, a shrimp and a polychaete.

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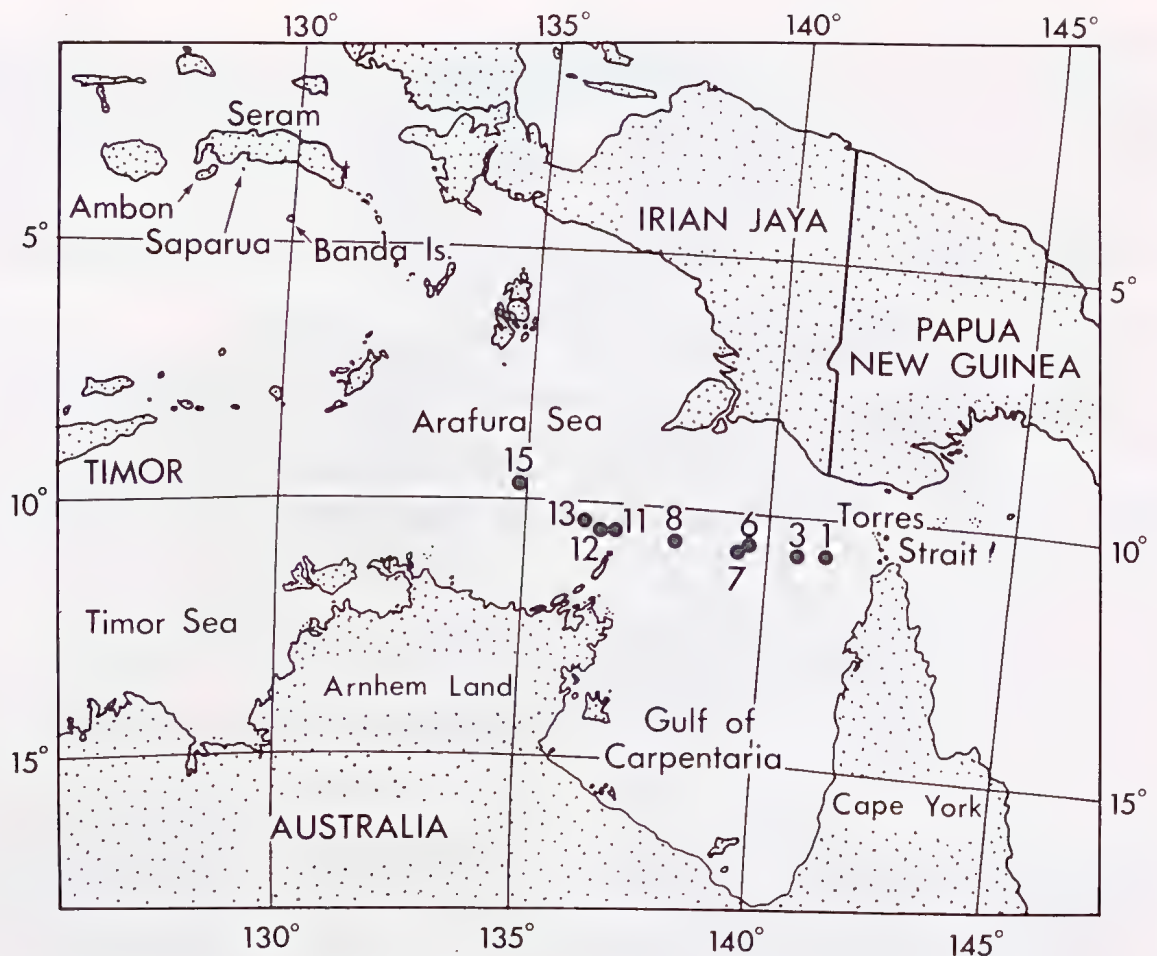


Fig.1. Area covered by the *Alpha Helix* Expedition.

During 1975 a joint United States-Australian-Indonesian expedition visited North Australian and Indonesian waters aboard the R.V. *Alpha Helix* for the purpose of studying various aspects of bioluminescence and the distribution and physiology of midwater animals. E. Ball joined the expedition in Cairns, Australia and collected hermit crabs from otter trawls in the Torres Strait and Arafura Sea (Fig. 1) as well as during visits to the islands of Saparua and Seram in Maluku. A station was established in the Banda Islands (Figs 1, 2), where a fairly comprehensive survey was made of the distribution, abundance and some aspects of natural history of the hermit crabs of the three small islands comprising this group.

The Banda Islands are relatively isolated volcanic islands lying approximately 200 km southeast of Ambon. The inner group consists of three islands: Gunungapi, an active volcano with an elevation of approximately 655 m; the neighbouring island of Naira on which stands the town of Bandanaira; and Banda Besar, which appears to be part of the wall of an ancient crater. The arrangement of these islands is such (Fig. 2) that they provide a wide variety of habitats ranging from almost totally protected

through protected areas with strong tidal currents to completely exposed coast. Associated with this diversity in exposure is a great diversity in substratum types which include mud, sand, fine gravel and coral rubble, living coral, cobbles and solid rock. Away from the inner group of islands the bottom falls away quite sharply down the old crater walls. Sea water temperatures during the expedition were in the range $28 \pm 1^\circ \text{C}$, although on some calm days higher temperatures would have been reached on the reef flats and in tidepools.

Materials and Methods

Hermit crabs were collected by otter trawl (in the Arafura Sea) and by SCUBA diving, free diving and intertidal collecting. Relative abundance, depth of collection and substratum were routinely recorded, as were any other factors felt to be of potential significance in relation to hermit crab natural history. Low oxygen levels, produced by keeping the animals together in a small volume of water, frequently caused them to emerge partly or completely from their shells. Alternatively, or when

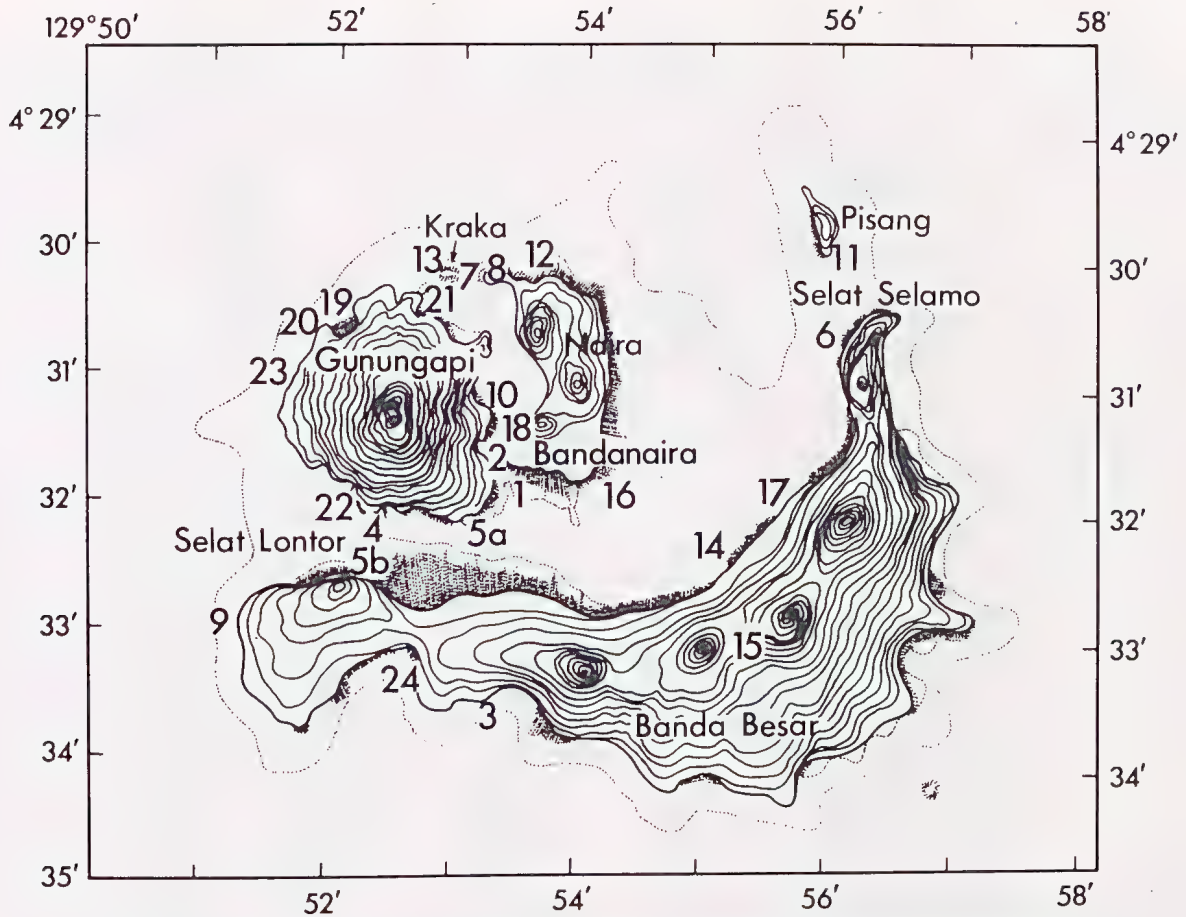


Fig.2. Map of Banda Islands, with collecting stations. Reef flats are shaded, land contours are shown at 30m intervals, outer dotted line marks 100m depth.

this method failed, animals were cracked from their shells with a vise. Colour was noted before the crabs were placed in preservative.

The collection was shipped to the Allan Hancock Foundation, where J. Haig made final identifications and prepared descriptions of new species. In general, these descriptions follow the format and terminology used in a series of papers by P.L. McLaughlin and collaborators (e.g. McLaughlin, 1974, 1975, 1986; McLaughlin & Provenzano, 1974; Haig & McLaughlin, 1984; McLaughlin & Haig, in press). Holotypes of new species are deposited in the Indonesian National Institute of Oceanology, Jakarta (NIOJ). Other material is deposited in the Crustacea collections of that institution and in those of the Australian Museum, Sydney (AM) and the Allan Hancock Foundation, Los Angeles (AHF).

For each species collected, we give the reference to its original description and to those of its junior synonyms, and to the work which first cited the name in its currently accepted combination. We also include references to other works which have important descriptive material or information on colour or behaviour. The general distribution of each species is also noted. Detailed station data are given in Table 1.

Keys are provided to the families and genera of hermit crabs that are known to occur in Maluku and to the species of certain genera (*Coenobita*, *Calcinus*, *Clibanarius* and *Dardanus*) which are common in that area. Since very little is known as yet about east Indonesian hermit crabs from deeper waters, we have included only those taxa that have been recorded in the area (previously or in the present paper) in depths of 20 metres or less. In the keys, species recorded from Maluku but not collected there during the *Alpha Helix* expedition are marked with an asterisk.

The following abbreviations are used in the text and in legends to the figures: SL – shield length; TL – total length; P – pereopod; pl – pleopod; mxp – maxilliped. Institutions other than the three cited above are abbreviated BMNH – (British Museum [Natural History], London), IM – (Indian Museum, Calcutta), MNHN – (Muséum National d'Histoire Naturelle, Paris), SMF – (Natur-Museum Senckenberg, Frankfurt am Main), and USNM – (National Museum of Natural History, Washington, D.C.). For the current spelling of Indonesian place names we have followed "Gazetteer of Indonesia" (Third Edition, 1982, Defense Mapping Agency, Washington, D.C.).

Table 1. Station data for material collected

ARAFURA SEA				
STATION (Alpha Helix)	LOCALITY	POSITION		DATE (1975)
		S	E	
1	Torres Strait	10°38.0'	141°06.5'	16 Mar
3	Torres Strait	10°39.0'	140°29.5'	16 Mar
6	Torres Strait	10°38.0'	139°27.0'	16 Mar
7	Torres Strait	10°40.2'	139°19.2'	16 Mar
8	Arafura Sea	10°29.2'	138°03.4'	17 Mar
11	Arafura Sea	10°27.5'	136°47.0'	17 Mar
12	Arafura Sea	10°26.0'	136°25.8'	17 Mar
13	Arafura Sea	10°15.2'	136°07.3'	17 Mar
15	Arafura Sea	09°32.3'	134°49.0'	18 Mar
BANDA ISLANDS				
STATION	LOCALITY	POSITION (APPROX.)		DATE (1975)
		S	E	
1	Naira, off Bandanaira town	4°32.0'	129°53.3'	25 Mar, 11,18 Apr
2	Naira, in Zonnegat off Bandanaira town	4°31.8'	129°53.2'	26 Mar
3	south side Banda Besar	4°33.7'	129°53.2'	27 Mar
4	south coast Gunungapi	4°32.3'	129°52.2'	28 Mar
5a	south side Gunungapi, north side of Selat Lontor	4°32.2'	129°53'	7 Apr, 6 May
5b	north side Banda Besar, south side of Selat Lontor	4°32.2'	129°53'	7 Apr
6	north-east tip Banda Besar	4°30.5'	129°56'	8 Apr
7	off Pulau Mati	4°30.1'	129°53'	9 Apr
8	north-west tip Pulau Naira	—	—	10 Apr
9	west end Banda Besar	4°32.6'	129°52'	12 Apr
10	east shore Gunungapi	4°31.3'	129°53.5'	13,25, 27 Apr
11	south-east end Pisang	4°30'	129°55'	18 Apr
12	north end Pulau Naira	4°30.1'	129°53.5'	21,24, 26 Apr
13	west side Kraka	4°30.1'	129°53'	22 Apr
14	off Combir on north side Banda Besar	—	—	23,24 Apr
15	Banda Besar, inland	4°33.5'	129°52'	24 Apr
16	Naira, off Pandeceru (no specimens collected)	—	—	25 Apr
17	Banda Besar (no specimens collected)	—	—	25 Apr
18	off Naira	4°31.4'	129°53.6'	27,30 Apr
19	outside of Gunungapi	4°30.3'	129°52.3'	28,30 Apr
20	outside of Gunungapi, protected bay	4°30.3'	129°52.5'	28 Apr, 4-5 May
21	shore of Gunungapi, approx. opposite Kraka	4°30.4'	129°52.8'	1 May
22	Gunungapi	4°32'	129°51.9'	3 May
23a	west side Gunungapi	4°31.2'	129°51.5'	4 May
23b	west side Gunungapi	4°31.2'	129°51.5'	4 May
24a	south-west end Banda Besar, large bay	4°33.3'	129°52.5'	7 May
24b	south-west end Banda Besar, large bay	4°33.3'	129°52.5'	7 May
SERAM, SAPARUA AND AMBON				
STATION	LOCALITY	POSITION (APPROX.)		DATE (1975)
		S	E	
Seram				
1	Village of Pohon Batu	2°57.7'	128°06.9'	30-31 Mar
2	Around Pulau Marsegu	3°00'	128°02.5'	31 Mar, 1 Apr
Saparua				
1	Pulau Saparua	3°36'	128°39.5'	29 Mar
2	Pulau Saparua	3°36.7'	128°39'	29 Mar
3	off Pulau Saparua	3°37.9'	128°38.6-39'	29 Mar
Ambon				
1	2 km east of Latu Halat, 15 km south-west of Ambon town	3°46.4'	128°08.2'	23 Mar

Historical Review

Previous work on hermit crabs from the areas covered by this report has been rather fragmentary. For the Arafura Sea and Torres Strait the most important collections were those of the *Alert* Expedition (Miers, 1884) and the *Challenger* Expedition (Henderson, 1888). Between them these expeditions collected eight species of hermit crabs from the Arafura Sea/Torres Strait region. Four of those species were taken again by the *Alpha Helix*, and another five species are now reported from the area for the first time.

Trawls were made around Banda during the *Challenger* Expedition of 1873–1876, but the only hermit crabs from that vicinity came from a depth of about 2600 metres. Collections were made at Banda during the *Siboga* Expedition of 1899–1900, the Danish Expedition to the Kei Islands in 1922, and the Voyage of T.R.H. the Prince and Princess Leopold of Belgium to the Netherlands East Indies in 1928–1929, but shallow water hermit crabs from those expeditions have not been reported upon as yet. However, Boschma (1931a), in a report on the Rhizocephala collected by Th. Mortensen in 1914–1916, cited a parasitised hermit crab, *Pagurus deformis* H. Milne Edwards (= *Dardanus deformis*) taken at Banda during the Kei Islands Expedition. Van Baal (1937) redescribed Boschma's rhizocephalans and again mentioned the host *D. deformis* from Banda. Although *D. deformis* has been recorded several times from eastern Indonesian waters, it was not among the species collected during the *Alpha Helix* Expedition.

Reyne (1938), in an historical account of the distribution of the robber or coconut crab *Birgus latro* (Linnaeus), cited records from Banda, including early collections by G.E. Rumphius and P. Bleeker.

We know of only one other previous record of a hermit crab from Banda. De Man (1881b) discussed a specimen of *Pagurus varipes* Heller from Naira; Lewinsohn (1969) re-examined this specimen and found it to be *Dardanus pedunculatus* (Herbst). *D. pedunculatus* was not taken at Banda during the *Alpha Helix* Expedition, although we report it from Seram and Saparua.

From the latter island a single species, *Birgus latro*, has been reported (see Reyne, 1938). The hermit crab fauna of Seram was previously represented by five species. Again, Reyne (1938) cited records of *Birgus latro*. Hilgendorf (1869) mentioned material of *Coenobita cavipes* Stimpson (as *C. violaceus*). Rathbun (1910) reported *Coenobita rugosus* H. Milne Edwards among decapods collected in 1906–1907 by T. Barbour. Van Kampen & Boschma (1925) and Boschma (1931b) recorded *Dardanus deformis* from the *Siboga* Expedition as the host of a rhizocephalan. *Clibanarius longitarsus* (De Haan) was collected at Seram during the *Snellius* Expedition (Buitendijk, 1937).

Alpha Helix records of several species treated in this report have already been noted in the literature. Humes (1981), in a paper on harpacticoid copepods of the expedition, recorded eight hermit crab hosts from Banda and Seram, and Forest (1984) included *Alpha Helix* material of *A. retipes* from Banda in his revision of the genus *Aniculus*.

Systematic Account

Key to Families of Hermit Crabs of Maluku Occurring in 20 Metres or Less

1. Antennular flagella truncated at tip; crabs terrestrial or semiterrestrial ... Coenobitidae
- Antennular flagella terminating in a filament; crabs marine 2
2. Outer maxillipeds usually contiguous at base; chelipeds equal or subequal, or left distinctly the larger Diogenidae
- Outer maxillipeds widely separated at base; left cheliped never larger than right, right usually much the larger Paguridae

Family COENOBITIDAE

Key to Genera and Species of Coenobitidae of Maluku

1. Rostrum prominent; posterior carapace greatly expanded laterally; abdomen well calcified, straight and symmetrical; animal living without shell (except in glaucothoe and young crab stages) *Birgus latro*
- Rostrum almost obsolete; posterior carapace not much expanded laterally; abdomen soft and spirally coiled; animals living in shells: *Coenobita* 2

2. Antennal acicle not fused with second segment of peduncle; ocular peduncles subcylindrical; a brush of setae on inner surface of right chela only *C. brevimanus*
- Antennal acicle fused with second segment of peduncle; ocular peduncles strongly compressed laterally; a brush of setae on inner surface of both chelae 3
3. Propodus of left pereopod 3 with outer surface flattened, this surface marked off from upper surface by a sharp ridge 4
- Propodus of left pereopod 3 with outer surface convex and not separated from upper surface by a ridge 5
4. Left chela with stridulating apparatus on upper part of outer surface; coxa of right pereopod 5 moderately produced in males *C. rugosus*
- Left chela without stridulating apparatus; coxae of both pereopods 5 weakly produced in males *C. cavipes*
5. Pereopods 2 and 3 thickly covered with small corneous spines; coxae of pereopods 5 not strongly produced in males **C. spinosus*
- Pereopods 2 and 3 granulate; coxa of right pereopod 5 produced into a long, curved tube in males *C. perlatus*

Birgus Leach

Birgus latro (Linnaeus)

Cancer latro Linnaeus, 1767: 1049.

Birgus latro.—Leach, 1815: 337.—Alcock, 1905b: 150, pl. 16.

Remarks. A coconut crab with a carapace length of about 16 cm was brought into camp, but was not preserved because of its size. This specimen, which was uniform black in colour, had been captured at the northwest tip of Naira (Banda Stn 8).

The distribution of *Birgus* in Maluku, as elsewhere, is probably determined mainly by human predation.

Distribution. East coast of Africa to Line and Gambier Islands; absent from northern Indian Ocean (except Nicobar Islands and part of Andaman Islands) and from west part of Malay Archipelago. Previously recorded from Banda (see Reyne, 1938).

Coenobita Latreille

Coenobita brevimanus Dana

Coenobita clypeata var. *brevimanus* Dana, 1852: 473; 1855: pl. 30 fig. 4b.

Coenobita clypeatus.—Alcock, 1905b: 141, 142, pl. 15 figs 1, 1a.

Coenobita brevimanus.—Rathbun, 1910: 314.

Coenobita hilgendorfi Terao, 1913: 388.

Coenobita clypeata.—Fize & Serène, 1955: 5, 7, text fig. 1, pl. 1 fig. 1.

Material examined. BANDA Stn 3, 1♂ (NIOJ).

Colour in life. Shield and posterior carapace reddish purple with 3 dark brownish-purple,

longitudinal stripes (1 median, 2 lateral). Ocular peduncles, antennules and antennae uniform brown. Chelipeds uniform purplish brown. Pereopods 2 and 3 uniform purple.

Remarks. This specimen was found about 200 m inland.

Distribution. East coast of Africa to Line Islands and Tuamotu Archipelago.

Coenobita cavipes Stimpson

Coenobita cavipes Stimpson, 1858: 245; 1907: 200.

Coenobita violascens Heller, 1862: 524.

Coenobita cavipes.—Alcock, 1905b: 146, pl. 14 fig. 1.—Fize & Serène, 1955: 5, 30, text figs. 3B, 5, pl. 1 figs 4–6.

Material examined. BANDA Stn 15, 1♂ juv (NIOJ). SERAM Stn 1, 1♂, 4♀ (NIOJ, AM P37713, AHF). AMBON Stn 1, 2♀ (NIOJ).

Colour in life. Shield and posterior carapace with elaborate pattern of dark brown spots and streaks on almost white background. Ocular peduncles almost white or pale brown ventrally, darker laterally; cornea brown. Antennular peduncles brown; flagellum brown or nearly orange. Antennae uniform brown. Chelipeds dark brown, with broad white area at proximal end of merus and some white at proximal end of carpus; most of palm and dactyl white. Ground colour of pereopod 2 dark brown; oblique, broad white stripe at proximal end of merus; longitudinal white stripe on carpus; white area at both ends of propodus. Pereopod 3 with patches and bands of white on dark brown background.

Remarks. The individual from Banda was found on a muddy trail in fairly dense rain forest, elevation ca. 300 m, at least 1.5 km from the sea. Specimens

from Seram occurred intertidally, and those from Ambon inshore on stumps and under coconut husks.

Distribution. East coast of Africa and Indian Ocean through Malay Archipelago to Bismarck Archipelago, and north to Ryukyu and Mariana Islands.

***Coenobita perlatus* H. Milne Edwards**

Coenobita perlata H. Milne Edwards, 1837: 242.

Coenobita perlatus.—Alcock, 1905b: 145, pl. 14 figs 2, 2a.

Coenobita purpurea Stimpson, 1858: 245.

Coenobita perlata.—Fize & Serène, 1955: 5, 24, text figs 3C, 4, pl. 1 fig. 2.

Material examined. BANDA Stn 6, 1♀ juv (NIOJ).

Colour in life. Shield with reddish orange markings on off-white background; posterior carapace pale reddish. Ocular peduncles solid red orange. Antennules and antennae uniform reddish orange. Major cheliped with merus, carpus and proximal part of chela reddish; most of palm white; dactyl almost black. Minor cheliped mostly reddish orange; upper margin of palm rimmed with black. Pereopods 2 and 3 orange red, with reddish brown area at distal end of propodus and proximal end of dactyl.

Remarks. This specimen was collected just inshore from the beach.

Distribution. Western Indian Ocean to Line and Gambier Islands.

***Coenobita rugosus* H. Milne Edwards**

Coenobita rugosa H. Milne Edwards, 1837: 241.

Coenobita rugosus.—Alcock, 1905b: 141, 143, pl. 14 figs 3, 3a.

Coenobita rugosa.—Fize & Serène, 1955: 5, 12, text figs 2, 3A, pl. 1 figs 3, 5, 7–10.

Material examined. BANDA Stn 3, 1♂ juv (NIOJ); Stn 6, 5♂, 4♀, 3 juv (NIOJ); Gunungapi, coll. A.G. Humes, 17♂, 12♀ (6 ov) (NIOJ, AM P37719, AHF). AMBON Stn 1, 5♂, 1♀ (NIOJ, AM P37732, AHF).

Colour in life. Carapace uniform pale brown. Ocular peduncles gray or brown, with brown cornea. Antennules and antennae uniform brown. Chelipeds pale brown or gray brown, with dark brown longitudinal streaks on carpus and chela, and dark band at distal end of merus. Pereopod 2 with merus very pale brown, dark brown ring at distal end; carpus, propodus and dactyl pale brown, carpus sometimes with longitudinal stripes. Pereopod 3 uniform pale brown, sometimes with dark brown spot at distal end of merus.

Remarks. Members of this species were found most abundantly on the beaches. At Ambon specimens were encountered inshore on stumps and under coconut husks.

Distribution. East coast of Africa to Line Islands and Tuamotu Archipelago.

Family DIOGENIDAE

**Key to Genera of Diogenidae of Maluku
Occurring in 20 Metres or Less**

1. Paired pleopods in both sexes (usually 2 pairs in males, 1 in females); chelipeds usually equal or subequal in size and form *Paguristes*
 — No paired pleopods in either sex 2
2. Fingers opening and closing horizontally; chelipeds equal or subequal *Clibanarius*
 — Fingers opening and closing obliquely or nearly vertically 3
3. Fingertips corneous and blackened 4
 — Fingertips calcareous; left cheliped much larger than right 6
4. Tips of fingers somewhat spooned; left cheliped usually much larger than right, the two occasionally subequal *Dardanus*
 — Tips of fingers hoof shaped; chelipeds equal or subequal 5
5. Cardiac region of carapace with a transverse groove; no stridulating apparatus on inner surface of chelae *Aniculus*
 — No transverse groove on cardiac region of carapace; inner surface of chelae with stridulating apparatus *Trizopagurus*
6. Telson without median transverse constriction; rostrum replaced by intercalary spine or scale between ocular acicles, this sometimes very small or obsolescent *Diogenes*
 — Telson with median transverse constriction; no intercalary process between ocular acicles *Calcinus*

Aniculus Dana*Aniculus erythraeus* Forest, 1984

Aniculus erythraeus Forest, 1984: 21, 41, figs 12, 19, 41–45.

Material examined. BANDA Stn 13, 1♀ juv (NIOJ).

Colour in life. Carapace and abdomen reddish purple and white. Ocular peduncles reddish purple; some white spots at base of setae. Antennular peduncles reddish purple with white spots and long, red and white setae; flagellum with lighter and darker bands of purple. Antennal peduncles reddish purple with white spots; flagellum uniform reddish purple. Chelipeds reddish purple with white tubercles, latter tipped with black spines; setae red with white tips. Pereopods 2 and 3 reddish purple; propodus and, to lesser degree, carpus with white area at proximal end of segment; setae red with white tips.

Remarks. The crab was found under a large block of dead coral in about 3 m of water.

Dr J. Forest examined this small (SL 6.2 mm) specimen but did not mention it in his recent revision of the genus *Aniculus*, not being sure of its identity. Now, however, he is almost certain that it is *A. erythraeus* (J. Forest, personal communication to J. Haig).

Distribution. Red Sea and Sri Lanka; and herein recorded from Banda, Indonesia.

Aniculus retipes Lewinsohn

Aniculus retipes Lewinsohn, 1982a: 76, fig. 1.—Forest, 1984: 20, 21, 51, figs 13, 20, 51–58.

Material examined. BANDA Stn 9, 1♀ (NIOJ); Stn 12, 2♂, 1♀ (NIOJ, AM P37737, MNHN).

Colour in life. Carapace red and white. Eyescales red. Ocular peduncles green or white, with 4 longitudinal brown stripes (one each dorsal, ventral, mesial and lateral); cornea brown. Basal segment of antennular peduncles pale green, distal segment yellow with green stripe dorsally; flagellum yellow. Antennal flagella uniform transparent purple. Chelipeds mostly red; carpus and distal part of merus brown. Merus, carpus and propodus of pereopods 2 and 3 pale red in proximal half, green distally; dactyl green; all 4 segments with 2 thin, longitudinal dark red lines; setae red with white tips.

Remarks. These crabs were taken at depths of 5–10 m in fairly exposed areas, on coral and on a bottom of rock, coral and coral rubble. They have already been recorded by Forest (1984).

Distribution. Red Sea, Tanzania, western Malay Peninsula, Vietnam, Banda and Samoa.

Calcinus DanaKey to Species of *Calcinus* Known from Maluku

1. Right chela with upper margin smooth or granulate. Pereopods 2 and 3 with coloured longitudinal stripe on merus and carpus; dactyl with coloured subdistal ring and subproximal spot *C. laevimanus*
 — Right chela with upper margin spinous or tuberculate 2
2. Pereopod 3 with dense brush of setae ventrally on dactyl and distal part of propodus 3
 — Pereopod 3 without dense brush of setae ventrally 4
3. Right cheliped with 2 or more spines distally on lower outer margin of merus. Merus, carpus and propodus of pereopods 2 and 3 each with broad coloured bands *C. elegans*
 — Right cheliped with 1 spine distally on lower outer margin of merus. Pereopods 2 and 3 coloured but without bands *C. gaimardii*
4. Ocular acicles simple. Dactyl of pereopods 2 and 3 with coloured band at proximal end *C. latens*
 — Ocular acicles multispinous 5
5. Pereopods 2 and 3 with longitudinal stripes or streaks 6
 — Pereopods 2 and 3 without longitudinal markings 7
6. Pereopods 2 and 3 with coloured longitudinal spots or streaks on all segments; carpus of pereopod 2, but not of pereopod 3, nearly covered by broad coloured band *C. pulcher*
 — Pereopods 2 and 3 with carpus and dactyl coloured but without longitudinal markings; propodus with longitudinal coloured stripes *C. undescribed sp.*

7. Ocular peduncles with broad coloured band; dactyl of pereopods 2 and 3 with coloured, white-spotted band proximally *C. guamensis*
 — No coloured band on ocular peduncles; dactyl of pereopods 2 and 3 solidly coloured, other segments with small coloured dots *C. minutus*

Calcinus elegans (H. Milne Edwards)

Pagurus elegans H. Milne Edwards, 1836: 278, pl. 13 fig. 2.
Pagurus pictus Owen, 1839: 83, pl. 25 figs 2, 2a.
Pagurus decorus Randall, 1839: 134.
Calcinus elegans.—Dana, 1852: 458; 1855: pl. 28 figs 10a–c.—Alcock, 1905b: 55, pl. 5 fig. 2.

Material examined. BANDA Stn 3, 1♂, 2♀ (1 ov) (NIOJ, AHF); Stn 24a, 1♂, 1♀ (AM P37746). SAPARUA Stn 3, 1♀ (NIOJ).

Colour in life. Carapace mottled with shades of brown and white. Ocular peduncles bright blue with narrow dark brown area at base; cornea black. Antennules and antennae uniform orange. Chelipeds dark brown with white tubercles on fingers and distal part of palm. Merus and carpus of pereopods 2 and 3 bright blue in proximal and dark brown in distal half; propodus blue at both ends, with broad, dark brown band medially; dactyl bright blue with dark brown spots, with narrow white band next to claw; dactyl and propodus with bright red setae ventrally.

Remarks. This species was collected in the shallow subtidal, on bottoms of coral and rock.

In the Hawaiian Islands, the brightly coloured bands on the second and third pereopods of *C. elegans* are orange instead of blue (Haig & McLaughlin, 1984: 108). This colour shift to orange has not been reported from any other locality within the range of the species.

Distribution. East coast of Africa to Hawaiian Islands and Tuamotu Archipelago. This species appears to have been rarely collected in the Indonesian area and it is now reported from Maluku for the first time.

Calcinus gaimardii (H. Milne Edwards)

Pagurus gaimardii H. Milne Edwards, 1848: 63.
Calcinus gaimardii.—Dana, 1852: 457; 1855: pl. 28 fig. 9.—Alcock, 1905b: 53, 56, pl. 5 fig. 3.
Calcinus gaimardi.—Fize & Serène, 1955: 40, 49, text figs 7, 8, pl. 2 figs 5–8.—Humes, 1981: 5.

Material examined. BANDA Stn 1, 1♀ (NIOJ); Stn 3, 2♂, 1♀, 2 juv (AHF); Stn 4, 1♂ (AM P37720); Stn 5b, 1♂, 3♀ (1 ov) (NIOJ); Stn 9, 2♂ (AM P37703); Stn 12, 2♂, 5♀ (AM P37704, AM P37722, AHF); Stn 13, 1 juv (NIOJ); Stn 14, 1♀, 1 juv (AHF); Stns 16, 17 (none collected); Stn 19, 2♂, 4♀ (1 ov), 1 juv (NIOJ, AHF); Stn 21, 4 juv (AM P37727); Stn 23a, 1 juv (AHF); Stn 24a, 6♂, 4♀, 3 juv (NIOJ); Stn 24b, 1♂, 1♀, 1 juv (AM P37718); Gunungapi, coll. A.G. Humes, 1♂ (AHF). SERAM Stn 2, 7♂, 4♀ (1 ov) (NIOJ, AM P37714, AHF). SAPARUA Stn 3, 2♂, 1♀ (NIOJ).

Colour in life. Shield white with shadings of green and brown, or dark brown with large whitish patch posteriorly; posterior carapace mottled green and white. Ocular peduncles dark brown proximally, with varying amounts of blue distally; cornea black with white spots. Antennules brown with orange flagellum; terminal segment of peduncle orange distally, shading to brown proximally. Antennae uniform orange. Chelipeds uniform brown; tips of fingers white. Pereopods 2 and 3 uniform brown; dactyl with narrow white band next to claw. In young specimens, proximal part of propodus of pereopods 2 and 3 brown, distal part white; dactyl white; both of these segments with brown dots.

Remarks. This species occurred nearly everywhere, usually in depths of less than 5 m on bottoms of coral, sand, and rocks.

Several specimens were parasitised by rhizocephalans. A male from Gunungapi was the host of copepods (Humes, 1981), and a female from Seram had a pair of bopyrids, *Propseudione rhombicosoma* Shiino, in one branchial chamber.

Distribution. East coast of Africa to Hawaiian and Society Islands.

Calcinus guamensis Wooster

Calcinus n.sp. 2.—Kropp *et al.*, 1981: 40.
Calcinus guamensis Wooster, 1984: 127, 141, fig. 4.—Haig & McLaughlin, 1984: 107, 108, 110.
 [?] *Calcinus latens*.—Miyake, 1956: 331, figs 20, 21. [not *C. latens* (Randall)]

Material examined. BANDA Stn 19, 8♂, 5♀ (2 ov), 1 juv (NIOJ, AM P37739, AM P37745, AHF); Stn 23a, 1♀ (NIOJ); Stn 24b, 1♂ (NIOJ).

Colour in life. Carapace white anteriorly, shading to purple posteriorly. Ocular peduncles white, with broad black or dark brown band; cornea black with white spots. Antennular peduncles with basal segment black, terminal segment greenish black to light green. Antennae solid orange. Merus of chelipeds white proximally, brown or black with white spots in distal half; carpus black or brown with white spots; palm gray or gray green; fingers white. Pereopods 2 and 3 white or grayish white, except for white-spotted black or brown band at proximal end of dactyl.

Diagnostic colour pattern lost rather quickly following preservation in alcohol.

Remarks. These small crabs were found mainly on cobbles in relatively exposed areas, in depths of 0–15 m.

Distribution. Recorded from Mariana and Hawaiian Islands; probably Ryukyu Islands (Miyake, 1956 as *Calcinus latens*, see Haig & McLaughlin, 1984: 108) and herein recorded from Maluku, Indonesia.

Calcinus laevimanus (Randall)

Pagurus laevimanus Randall, 1839: 135.

[?] *Pagurus lividus* H. Milne Edwards, 1848: 63.

Calcinus herbstii De Man, 1888: 437.—Alcock, 1905b: 53, pl. 5 fig. 4.

Calcinus laevimanus.—Rathbun in Stimpson, 1907: 208 (footnote).

Calcinus herbsti.—Fize & Serène, 1955: 40, 41, text fig. 6, pl. 2 figs 1–4.

Material examined. BANDA Stn 5b, 2♂ (AM P37717); Stn 24a, 3♂, 1♀ (NIOJ, AHF).

Colour in life. Carapace greenish white or gray green. Ocular peduncles with basal half blue, distal half orange; cornea blue or brown. Antennules blue except for narrow orange band at distal end of basal article; flagellum orange. Antennal peduncles with basal segment and acicle blackish green, rest of peduncle and flagellum orange. Chelipeds dark brown; fingers and distal part of palm with varying amounts of white. Pereopods 2 and 3 with ground colour of merus and carpus brown or golden, propodus brown or greenish brown; dark brown longitudinal stripe on merus and carpus; dactyl white, with brown or dark green subdistal ring and subproximal spot.

Remarks. The crabs were collected in the intertidal or shallow subtidal on bottoms of sand and rock.

Specimens from both stations were infected by rhizocephalan parasites. One individual from Station 5b bore a pair of abdominal bopyrids, *Parathelges weberi* Nierstrasz & Brender à Brandis.

Distribution. East coast of Africa to Hawaiian Islands and Tuamotu Archipelago.

Calcinus latens (Randall)

Pagurus latens Randall, 1839: 135.

Pagurus cristimanus H. Milne Edwards, 1848: 64.

Calcinus latens.—Dana, 1852: 459; 1855: pl. 28 fig. 11.—Alcock, 1905b: 55, 58, pl. 5 fig. 5.—Fize & Serène, 1955: 40, 58, text fig. 9, pl. 2 figs 9–11.—Humes, 1981: 5, 7.—Haig & McLaughlin, 1984: 107, 108, 109.

Calcinus intermedius De Man, 1881a: 102.

Calcinus terrae-reginae Haswell, 1882: 760.—Alcock, 1905b: 53, 57, pl. 5 fig. 7.

Material examined. BANDA Stn 1, 1♀ (NIOJ); Stn 5a, 1 intersex (AM P37725); Stn 5b, 12♂, 6♀ (1 ov), 1 juv (AHF); Stn 10, 1♂, 1♀, 4 juv (NIOJ, AHF); Stn 12, 2♂, 1♀ (NIOJ); Stn 14, 3♂, 1♀, 2 juv (NIOJ); Stn 18, 4 juv (NIOJ); Stn 24a, 3♂, 5♀ (3 ov), 3 juv (AM P37728); Gunungapi, coll. A.G. Humes, 11♂, 4♀ (2 ov) (NIOJ, AM P37726).

Colour in life. Shield dark greenish black, shading off to mottled green and white. Ocular peduncles

uniform greenish pink or pale purplish brown; cornea black with white spots. Basal segment of antennular peduncles blue; distal segment orange with proximal brown streak dorsally, or brown proximally and blue distally; flagellum orange. Antennal peduncles green, flagellum uniform yellow green. Merus and carpus of chelipeds dark green or black with few scattered white tubercles; chela black proximally, gradually graying to white distally; fingers white. Merus and carpus of pereopods 2 and 3 very dark green or dark brown black, with white tubercles; propodus much lighter gray green, or brownish purple proximally and white distally; dactyl white, with deep purple band at proximal end.

Remarks. These hermit crabs were found essentially everywhere, usually on rocks or sand in less than 3 m, and frequently were very abundant. Rhizocephalans were found in association with them at several localities; one parasitised crab from Station 5a had both male and female gonopores. The specimens collected by A.G. Humes in 15 m were the hosts of copepods (Humes, 1981).

Haig & McLaughlin (1984: 107), in a discussion of the live colouration of *Calcinus latens* in Hawaii, noted that in those islands the proximal purple band on the dactyl of the walking legs is formed by short longitudinal stripes of blue and dark violet. This pattern is evident in preserved specimens from Maluku where the colours appear as a pale bluish purple band overlaid by short longitudinal stripes of dark red, although a solid deep purple band was noted in the living animals. Haig & McLaughlin (1984: 108) point out that several authors have reported a solid band of colour on the dactyl of the walking legs in *C. latens*. This is probably typical of live specimens in most parts of the Indo-West Pacific.

Distribution. Red Sea and east coast of Africa to Hawaiian and Gambier Islands.

Calcinus minutus Buitendijk

Calcinus minutus Buitendijk, 1937: 269, figs 13–15.—Forest, 1958: 185, figs 1, 6–8, 14, 18.—Nakasone, 1975: 3, fig. 2.—Humes, 1981: 5, 7.

Material examined. BANDA Stn 2, 2♂, 3♀ (AHF); Stn 4, 1♂, 3♀ (1 ov), 1 juv (AM P37724); Stn 7, 1♂ (AM P37729); Stn 9, 2♂, 3♀ (AHF); Stn 10, 1♂ (NIOJ); Stn 12, 1♂, 1♀ (AM P37705); Stn 13, 2♀ (NIOJ); Stn 19, 5♂, 4♀ (2 ov), 1 juv (NIOJ, AM P37706); Stn 20, 1♀, 1 juv (AHF); Stn 23a, 1♂, 2♀ (AM P37723); Stn 23b, 1♂, 2 juv (AHF); Gunungapi, coll. A.G. Humes, 4♂, 3♀, 1 intersex (NIOJ, AM P37715). SERAM Stn 2, 1♂, 2♀ (NIOJ, AHF). PULAU GOMUMU south of Obi, coll. A.G. Humes, 1 intersex (NIOJ).

Colour in life. Shield uniform white; posterior carapace mottled pink and yellow. Ocular peduncles uniform white; cornea black with white spots. Mouthparts black. Basal antennular segments black; distal segment black proximally and white distally;

flagellum brown. Antennal flagella transparent pale brown. Chelipeds uniform white, or rarely delicate pale purple. Merus, carpus and propodus of pereopods 2 and 3 white with scattered, small orange dots; dactyl bright orange.

Remarks. This species was found nearly everywhere down to depths of about 15 m, almost always on coral and was sometimes very abundant. Rhizocephalans and copepods (Humes, 1981) were associated with or parasitised this species.

Distribution. Red Sea; Vietnam north to Ryukyu Islands and southern Japan; eastern Malay Archipelago; north-eastern New Guinea, Palau Islands, West Caroline Islands, and Mariana Islands.

Calcinus pulcher Forest

Calcinus pulcher Forest, 1958: 287, figs 4, 12, 13, 16.—Baba, 1982: 65.

Material examined. BANDA Stn 2, 4♂ (NIOJ, AM P37755, AHF); Stn 14, 1♀ (NIOJ). SERAM Stn 2, 4♂, 4♀ (NIOJ, AM P37756, AHF).

Colour in life. Shield light brown, with large, median dark brown spot behind rostrum; posterior carapace light brown, dark on edges. Ocular peduncles dark brown in about proximal half, shading to white distally; cornea black with white spots. Antennular peduncles with basal segment and proximal part of terminal segment brown; distal part of terminal segment blue; flagellum orange. Antennal flagella solid orange. Chelipeds brown, fingers and distal part of palm white; large dark brown spot on outer and inner surfaces of palm, closer to proximal than to distal end of segment. All segments of pereopods 2 and 3 with many black, somewhat elongate longitudinal spots or streaks on white background; merus sometimes with median black band, incomplete on outer surface; carpus of pereopod 2, but not of pereopod 3, with very broad, bright red band covering almost entire segment;

propodus with subdistal black band; dactyl with median black band.

Remarks. At Banda this species was found only in protected areas at depths of about 3–8 m on coral, sand and rocks. Two specimens from Seram were parasitised by rhizocephalans.

Distribution. Vietnam, Palau Islands and southern Japan; now Maluku in Indonesia.

Calcinus undescribed sp.

Calcinus aff. *pulcher*.—Eldredge *et al.*, 1979: 18, 60.—Kropp & Eldredge, 1982: 126.

Calcinus sp. 1 [aff. *pulcher*].—Kropp *et al.*, 1981: 40.

Calcinus sp. undescribed.—Humes, 1981: 5.

Calcinus sp. 1.—Wooster, 1984: 126, 138.

Remarks. Forty-eight specimens were found at Banda and Seram in about 3–15 m on coral and rock. Several of them were parasitised by rhizocephalans. An individual from Banda Station 9 had a pair of bopyrids, *Parapagurion calcinicola* Shiino, in one branchial chamber; another crab from the same station bore an abdominal bopyrid, an undescribed species of *Athelges*; and a specimen from Banda Station 19 was parasitised by an abdominal bopyrid, *Anathelges muelleri* Nierstrasz & Brender à Brandis. Two specimens collected by A.G. Humes were the hosts of copepods (Humes, 1981).

This species, which will be described elsewhere, is closely allied to *Calcinus pulcher* Forest but can be immediately distinguished from it by details of the colour pattern on pereopods 2 and 3. In the undescribed species the dactyl of those legs, and the carpus of both pereopods 2 and 3, are red without dark longitudinal streaks, and there are three well defined, dark longitudinal stripes on the outer and inner surfaces of the propodus.

Distribution. Maluku, Mariana Islands and Eastern Caroline Islands.

Clibanarius Dana

Key to Species of *Clibanarius* Known from Maluku

1. Pereopods 2 and 3 with well-defined, longitudinal coloured stripes on merus, carpus and propodus 2
- No well-defined, longitudinal coloured stripes on pereopods 2 and 3 (except on dactyl in certain species). Dactyl of pereopod 3 usually distinctly shorter than propodus, occasionally the 2 articles about the same length 7
2. Dactyl of pereopod 3 distinctly shorter than propodus. Ocular peduncles and carapace shield with longitudinal coloured stripes; dactyl of pereopods 2 and 3 pale in typical variety, with longitudinal coloured stripe on outer face in var. *rhabdodactylus* **C. zebra*
- Dactyl of pereopod 3 usually longer than propodus, sometimes about same length as propodus or slightly shorter 3

3. Ocular peduncles with longitudinal coloured stripe 4
 — No longitudinal coloured stripe on ocular peduncles 5
4. Carapace flattened; coxae of pereopods 4 and 5 broadly separated *C. eurysternus*
 — Carapace not flattened; coxae of pereopods 4 and 5 approximated **C. padavensis*
5. Upper margin of palm with pointed tubercles. Outer face of pereopods 2 and 3 with 2 longitudinal coloured stripes, these frequently interrupted toward ends of segments **C. laevimanus*
 — Upper margin of palm with row of distinct spines 6
6. Antennular and ocular peduncles about equal in length. Outer face of pereopods 2 and 3 with median longitudinal stripe, this stripe pale with coloured margins *C. longitarsus*
 — Antennular peduncles shorter than ocular peduncles. Outer face of pereopods 2 and 3 with 2 longitudinal coloured stripes on paler coloured background ... **C. striolatus*
7. Chelipeds and pereopods 2 and 3 with many pale blotches and spots on coloured background 8
 — No conspicuous pale blotches and spots on pereopods 9
8. Propodus of left pereopod 3 with outer face flattened and densely setose ... *C. corallinus*
 — Propodus of left pereopod 3 with outer face not much flattened and not densely setose **C. cruentatus*
9. Propodus of pereopods 2 and 3 with well-defined pale area distally on outer face 10
 — No well-defined pale area distally on outer face of propodus of pereopods 2 and 3 12
10. Propodus of pereopod 2 with pale area confined to distal end, that of pereopod 3 forming broad pale band, frequently along entire length of segment ... **C. merguiensis*
 — No broad pale band along entire length of propodus of pereopod 3 11
11. Propodus of pereopods 2 and 3 with pale band at both ends of segment; dactyl pale, with longitudinal coloured stripe on dorsal and ventral margins and on outer face *C. boschmai*
 — Propodus of pereopods 2 and 3 with pale band at distal end only; dactyl pale, with longitudinal coloured streak or patch on dorsal and ventral margins but not on outer face *C. englaucus*
12. Ocular peduncles coloured, with narrow pale band next to cornea. Propodus of pereopods 2 and 3 solidly coloured, usually more deeply at distal end; dactyl pale, with or without submedian coloured ring *C. virescens*
 — Ocular peduncles coloured, with broad pale band distally and large pale patch proximally. Propodus of pereopods 2 and 3 pale, with dark area distally; dactyl pale, never with submedian ring **C. humilis*

***Clibanarius boschmai* Buitendijk**

Clibanarius boschmai Buitendijk, 1937: 261, 267, figs 10–12.—Fize & Serène, 1955: 77.

Material examined. SAPARUA Stn 3, 7♂, 2♀ (NIOJ, AM P37731, AHF).

Colour in life. Carapace cream to pale purple, with darker purple longitudinal markings. Ocular peduncles dark brown dorsodistally, mesially and

laterally, with white patch proximally on dorsal surface; cornea black with white spots. Basal segments of antennules dark brown, terminal segment of peduncle greenish brown, flagellum orange. Antennal flagella uniform orange. Chelipeds uniform dark brown; small dorsoproximal spot on chela; fingers mostly white. Merus of pereopods 2 and 3 white proximally, with rather narrow, uneven brown band distally; carpus dark brown, with uneven white band at both ends; propodus same, uneven

white bands broader than on carpus; dactyl blue except for narrow white area next to claw, blue area with dark brown longitudinal stripes (one each dorsal, ventral, mesial and lateral).

Remarks. The specimens were collected in 0–1 m on rocks.

Distribution. Reported only from Paternoster Islands (Kepulauan Tengah), Kisar and Leti in southeastern Indonesia. The Saparua record represents a small extension of range northward.

Clibanarius corallinus (H. Milne Edwards)

Pagurus corallinus H. Milne Edwards, 1848: 63.

Pagurus globoso-manus Dana, 1851: 271.

Clibanarius corallinus.—Dana, 1852: 468; 1855: pl. 29 figs 8a–e.—Alcock, 1905b: 43, 48, pl. 5 fig. 11.—Fize & Serène, 1955: 77, 132, fig. 20.

Material examined. BANDA Stn 5b, 2♀ (AHF); Stn 10, 1♂, 1♀ (NIOJ).

Colour in life. Shield brown; posterior carapace with 3 longitudinal white stripes on brown background. Ocular peduncles brown dorsally, orange laterally and mesially; cornea blue. Antennular peduncles brown, flagellum orange. Antennal flagella uniform orange. Chelipeds brown with white tubercles. Pereopods 2 and 3 solid brown.

Remarks. This species occurred intertidally or in the shallow subtidal in protected areas.

Distribution. Eastern Indian Ocean to Line Islands and Tuamotu Archipelago.

Clibanarius englaucus Ball & Haig

Clibanarius englaucus Ball & Haig, 1972: 97, fig. 5.

Material examined. BANDA Stn 3, 20♂, 15♀ (12 ov) (NIOJ, AM P37716, AHF); Stn 5b, 1♂ (AHF); Stn 24a, 7♂, 7♀ (2 ov) (NIOJ, AM P37709, AHF).

Colour in life. Carapace mottled gray green. Ocular peduncles orange, with brownish dorsal longitudinal stripe; cornea black with white spots. Antennular peduncles brownish, with tinge of blue at distal end of terminal segment; flagellum orange. Antennae predominantly red orange with most of basal peduncular segment brown. Chelipeds mostly brown; narrow zone of blue at base of fingers, latter mostly orange. Merus, carpus and most of propodus of pereopods 2 and 3 dark brown; distal end of propodus orange; dactyl with diffused, submedian blue band, white proximally and with brown area distally.

Remarks. These crabs occurred on rock in the intertidal or shallow subtidal, and were sometimes very abundant in exposed areas.

A few individuals were infected by rhizocephalan parasites. A female from Station 24a had a pair of bopyrids, *Asymmetrione asymmetrica* (Shiino), in one gill chamber.

Distribution. This species was previously known only from the type locality, Karkar Island off north-eastern New Guinea. Its range is now extended westward to the Banda Islands.

Clibanarius eurysternus (Hilgendorf)

Pagurus (Clibanarius) eurysternus Hilgendorf, 1879: 822, pl. 3 figs 9, 10.

Clibanarius eurysternus.—De Man, 1888: 447.—Fize & Serène, 1955: 76, 118, fig. 17.

Material examined. BANDA Stn 5b, 1♂ (NIOJ).

Colour in life. Carapace, ocular, antennular and antennal peduncles, chelipeds and pereopods 2 and 3 with alternating longitudinal stripes of white and dark brown or black. Antennal flagella with black and white bands. Abdomen mottled brown and white. Pattern as depicted by Fize & Serène (1955: fig. 17) and by Miyake (1956: figs 4, 5).

Remarks. This specimen was collected in a protected shallow water area with a current, on coral sand or rock in 0–5 m.

Distribution. East coast of Africa to Marshall and Gilbert Islands.

Clibanarius longitarsus (De Haan)

Pagurus longitarsus De Haan, 1849: 211, pl. 50 fig. 3.

Clibanarius longitarsis.—Dana, 1852: 464.

Clibanarius longitarsus.—Fize & Serène, 1955: 76, 83, text fig. 11A–C, pl. 3 figs 1, 7, 10, 13.

Material examined. SERAM Stn 1, 1♂ (NIOJ).

Colour in life. Whole animal muddy brown, appearing muddy even when clean. Carapace fairly uniform brown, lightening posteriorly. Ocular peduncles uniform, semi-transparent greenish brown. Antennular and antennal peduncles light brown dorsally, darker brown laterally. Chelipeds and pereopods 2 and 3 uniform muddy brown.

In preservative, pereopods 2 and 3 distinctly showing remains of blue longitudinal stripes with red borders, in pattern characteristic of *Clibanarius longitarsus* (Fize & Serène, 1955: 88–89).

Remarks. The crab was collected from a muddy shore.

Distribution. Red Sea, east coast of Africa, and Indian Ocean, through Malay Archipelago and north to Ryukyu Islands and Japan.

Clibanarius virescens (Krauss)

Pagurus virescens Krauss, 1843: 56, pl. 4 fig. 3.

Clibanarius virescens.—Dana, 1852: 466.—McCulloch, 1913: 346, 351, pl. 11 fig. 2.—Fize & Serène, 1955: 77, 138, fig. 21.

Calcinus astathes Stebbing, 1924: 239, pl. 2 (Crustacea pl. 117).

[?] *Clibanarius philippinensis* Yapchiongco in Estampador, 1937: 501.

Material examined. BANDA Stn 5b, 1♀ (NIOJ); Stn 24a, 1♀, 1 juv (NIOJ).

Colour in life. Carapace with shades of dark and light brown. Ocular peduncles solid olive drab or dark brown, except for narrow white ring just proximal to cornea; cornea black with white spots. Antennular peduncles with basal segment olive drab or dark brown, terminal segment olive drab or dark brown fading to orange distally; flagellum orange. Antennal flagella uniform blue or brown. Chelipeds olive drab or brown with white tubercles and white fingers. Pereopods 2 and 3 olive drab or dark brown, colour concentrated in darker band at distal end of propodus; dactyl white.

Remarks. This species was found in the intertidal or shallow subtidal on a bottom of coral, sand and rock.

Our specimens belong to the colour variety of *Clibanarius virescens* in which the dactyl of the second and third pereopods is yellow or white, without a submedian dark ring. In colour and morphology they also conform with the description of *C. philippinensis* Yapchiongco. Comparison of the description of the latter species with a good series of *C. virescens* in the Allan Hancock Foundation suggested that the two forms may be identical. The type material, along with other Philippine collections, was destroyed during World War II (Estampador, 1959: 1), and therefore we can only tentatively place *C. philippinensis* in synonymy with *C. virescens*.

Distribution. East coast of Africa to Ellice and Fiji Islands.

Dardanus Paul'son

Key to Species of *Dardanus* Known to Occur in Maluku

1. Cornea not occupying more than one-third of ocular peduncles 2
 — Cornea occupying more than one-third of ocular peduncles 6
2. Chelipeds covered with strong corneous spines 3
 — Chelipeds covered with small spines 4
3. Left cheliped distinctly longer than right; shield and pereopods covered with pale, ocellate spots *D. megistos*
 — Left cheliped not much longer than right; no ocellations on shield or pereopods *D. lagopodes*
4. Propodus and dactyl of left pereopod 3 with transverse striations on lateral surface *D. guttatus*
 — Propodus and dactyl of left pereopod 3 without transverse striations 5
5. Left chela with outer face granulose, upper margin with row of spines, lower margin unarmed **D. scutellatus*
 — Left chela decorated on outer face with small pointed spines, upper and lower margins spinulose *D. woodmasoni*
6. Propodus of left pereopod 3 with dorsal and lateral faces delimited by sharp crest on dorsolateral margin **D. deformis*
 — Propodus of left pereopod 3 without sharp crest on dorsolateral margin 7
7. Left chela with small rounded tubercles over entire outer surface *D. gemmatus*
 — Left chela with small rounded tubercles on upper half and smooth on lower half of outer surface *D. pedunculatus*

Dardanus gemmatus (H. Milne Edwards)

Pagurus gemmatus H. Milne Edwards, 1848: 60.—Forest, 1954: 557, figs 10, 11.
Dardanus gemmatus.—Holthuis, 1953: 48.

Material examined. BANDA Stn 5a, 1♂ (NIOJ); Stn 12, 1♂ (NIOJ); Stn 20, 1♂ (AHF). SERAM Stn 2, 1♂, 1♀ (NIOJ).

Colour in life. Shield mottled purple and white, with large patch of uniform orange brown medially, latter extending anteroposteriorly about three-quarters length of shield; posterior carapace mottled in shades of pale orange, purple and white. Ocular peduncles red, with median white band; cornea silver or greenish. Antennules dark red basally, lighter red

distally. Antennal peduncles purple; flagellum transparent reddish. Major cheliped dark orange purple or reddish purple proximally, paler distally; minor cheliped with varying shades of orange purple or reddish purple. Merus of pereopods 2 and 3 mottled purple and white; carpus, propodus and dactyl uniform pale orange with tinges of purple.

Remarks. All the specimens from Banda were collected in less than 2 m of water: two during the day under rocks and dead coral and one at night in the open. The crabs from Seram were found in 1–3 m.

Each of the five specimens had two species of anemones on its shell. *Calliactis polypus* (Forskål) is a large anemone with a brown and white striped column, purple and white banded tentacles, and white acontia around the base. A smaller, white species, presumably *Sagartiomorphe paguri* (Verrill), is always located near the opening of the shell. For the specimens from Banda, the number of individuals of each anemone associated with each *Dardanus* is as follows:

	<i>Calliactis</i>	<i>Sagartiomorphe</i>
Stn 5a	4	9
Stn 12	5	2
Stn 20	3	3

The association between *Dardanus gemmatus* and *Calliactis polypus* has been discussed in some detail by Ross (1970, 1975) and by Röss & Wada (1975).

Distribution. Western Indian Ocean to Hawaiian and Society Islands. We have found no published record of this species from the Indonesian area, although there is a single, indefinite designation "Malaysia" (Miers, 1880: 375).

Dardanus guttatus (Olivier)

Pagurus guttatus Olivier, 1812: 640.—Alcock, 1905b: 87, pl. 9 fig. 1.—Fize & Serène, 1955: 158, 159, 173, text fig. 26, pl. 5 figs 1–3.

Dardanus guttatus.—Holthuis, 1953: 48.—Humes, 1981: 3, 6, 7, 11.

Material examined. BANDA Stn 3, 1♂ juv (AHF); Stn 12, 1♀ ov, 1 juv (NIOJ); Stn 24a, 1♂, 1♀ juv, 1 juv (AM P37788, AHF). SERAM Stn 2, 1♂, 1♀ (NIOJ); Pulau Parang, eastern Seram, coll. A.G. Humes, 1♂ (AHF). SAPARUA Stn 2, 1♀, 1 juv (NIOJ). KARANG MIE, eastern central Halmahera, coll. A.G. Humes, 1♂ (NIOJ).

Colour in life. Shield with white spots on reddish purple background, anterior half with large green markings; posterior carapace mottled reddish purple and pale tan. Abdomen bright reddish purple with white spots, transparent ventrally. Ocular peduncles solid purplish brown or purplish pink, with narrow white line next to black cornea; acicles reddish purple with white spots. Antennules and antennae uniform purplish pink or transparent light brown. Chelipeds reddish purple with white spots; dorsal surface of carpus with large, dark green spot covering most of

segment; setae reddish purple with white tips. Second pereopods reddish purple with white spots; carpus with large, dark green spot like that on chelipeds. Third pereopods similar, but white spots usually elongate, forming broken band near distal and proximal ends of propodus.

Remarks. Most of the crabs were found in about 0–4 m on coral and rock. The specimens collected by A.G. Humes were hosts of copepods (Humes, 1981).

Distribution. East coast of Africa to Line Islands and Samoa.

Dardanus hessii (Miers)

Pagurus hessii Miers, 1884: 264, pl. 28 fig. A.—Alcock, 1905b: 93, pl. 8 fig. 4.

Pagurus similimanus Henderson, 1888: 59, pl. 6 fig. 6.

Pagurus hessi.—Fize & Serène, 1955: 158, 159, 214, text fig. 34, pl. 4.

Dardanus hessii.—Gordan, 1956: 314.

Material examined. ARAFURA Stn 7, 1♀ (AM P37708).

Colour in life. Ocular peduncles white dorsally, with broad purple longitudinal stripe mesolaterally; cornea green. Antennules and antennae white. Chelae white with brown fingers.

Remarks. Collected in 49 m; substrate unknown.

Distribution. Gulf of Oman, Maldives, India, Malay Peninsula, thence north to Vietnam, Taiwan and Japan; east through Malay Archipelago to Arafura Sea (the type locality) and Torres Strait.

Dardanus imbricatus (H. Milne Edwards)

Pagurus imbricatus H. Milne Edwards, 1848: 61.—Alcock, 1905b: 92, pl. 9 fig. 8.—Fize & Serène, 1955: 158, 159, 220, text fig. 35, pl. 6 figs 11–14.

Dardanus imbricatus.—Gordan, 1956: 314.

Material examined. ARAFURA Stn 1, 1♂, 1 juv (AM).

Colour in life. Ocular peduncles pale blue proximally, white distally, with narrow, reddish brown submedian band; cornea green. Antennules and antennae white. Chelae reddish, grading to white proximally; teeth on cutting edge of fingers purple. Dactyl of pereopods 2 and 3 reddish brown, other segments white.

Remarks. These crabs were collected in 27 m on an unknown substrate. The larger specimen had seven anemones on its shell, which was shared by a cirolanid isopod, *Neocirolana hermitensis* (Boone). We have not found any published records of an association of anemones with *Dardanus imbricatus*. The closely related species *D. arrosor* (Herbst) frequently bears anemones on its shell.

Distribution. Reported from Sri Lanka, Thailand and Vietnam; otherwise Australia (Western Australia, Northern Territory and northern Queensland), including Torres Strait.

Dardanus lagopodes (Forskål)

- Cancer lagopodes* Forskål, 1775: 93.
Pagurus sanguinolentus Quoy & Gaimard, 1824: 532, pl. 79 fig. 2.—Fize & Serène, 1955: 158, 159, 166, text fig. 25, pl. 4 figs 4, 5.
Pagurus affinis H. Milne Edwards, 1836: 274.
Pagurus euopsis Dana, 1852: 452; 1855: pl. 28 fig. 6a–c.—Alcock, 1905b: 80, 86, pl. 9 fig. 2.
Pagurus depressus Heller, 1861: 22.
Dardanus hellerii Paul'son, 1875: 90, pl. 12 figs 4, 4a–c; 1961: 96, pl. 12 figs 4, 4a–c.
Dardanus lagopodes.—Lewinsohn, 1969: 32, pl. 2.—Humes, 1981: 3, 6, 7, 11.

Material examined. BANDA Stn 1, 1♀ (AHF); Stn 4, 2♂, 4♀ (2 ov), 1 juv (AM P37752); Stn 5a, 1♂, 1♀ (AHF); Stn 5b, 1♂, 1♀ ov, 3 juv (NIOJ); Stn 7, 1♀ (AHF); Stn 9, 1♂, 2♀ ov, 8 juv (AM P37797); Stn 10, 2♂, 2♀, 3 juv (NIOJ); Stn 12, 1♀ (AM P37748); Stn 13, 1♂, 1 juv (AM P37751); Stn 14, 3♂, 2♀, 10 juv (NIOJ); Stn 18, 1 juv (AHF); Stn 19, 3♂, 1♀ (AM P37786, AHF); Stn 20, 1 juv (AHF); Stn 21, 1♂ (AM P37784); Stn 23a, 1 juv (AM P37738); Stn 23b, 1♂, 1♀, 1 juv (NIOJ); Stn 24a, 3♂, 1♀ (AHF); Gunungapi, coll. A.G. Humes, 5♂, 2♀ (NIOJ, AM P37787, AHF). SERAM Stn 2, 11♂, 4♀, 7 juv (NIOJ, AM P37735, AHF); Pulau Marsegu, western Seram, coll. A.G. Humes, 1♂ (NIOJ); Pulau Parang, eastern Seram, coll. A.G. Humes, 1♂, 1♀ (AM P37798, AHF). SAPARUA Stn 1, 1♂, 9 juv (NIOJ); Stn 3, 2♂, 1♀, 2 juv (NIOJ). KARANG MIE, east central Halmahera, coll. A.G. Humes, 1♂ (NIOJ). NATSEPA, Ambon, coll. A.G. Humes, 1♂ (NIOJ).

Colour in life (black form). Shield brownish purple, with large brown spot anteriorly; posterior carapace mottled bright red and tan. Ocular peduncles uniform purplish brown, with narrow yellow line next to black cornea. Antennules and antennae yellowish brown. Chelipeds reddish purple with white tubercles and white-tipped red setae. Pereopods 2 and 3 reddish purple; broad black band at distal end of merus and large black patch on carpus; setae reddish purple with white tips.

Black form frequently found together with red form, latter differing in having bright red patch on carpus of pereopods 2 and 3 (see Fize & Serène, 1955: 170; Ball & Haig, 1972: 92–93).

Remarks. This species was found everywhere, although never in really high densities, from just subtidal to at least 15 m.

At Banda Stations 1 and 5b and at Pulau Parang an alpheid shrimp, *Aretopsis amabilis* De Man, was found sharing the shell with the hermit crab. Other *Dardanus lagopodes* were parasitised by rhizocephalans or had copepods associated with them (Humes, 1981).

An individual found on dead coral in about 2 m of water at Banda Station 13 was observed feeding by scraping with both chelipeds at the mud and algae on the surface of the coral, then transferring the detritus to its mouth.

Distribution. Red Sea and east coast of Africa to Marshall and Gilbert Islands and Tuamotu Archipelago.

Dardanus megistos (Herbst)

- Cancer megistos* Herbst, 1804: 28, pl. 61 fig. 1.
Pagurus punctulatus Olivier, 1812: 641.—Alcock, 1905b: 81, pl. 8 fig. 1.
Pagurus spinimanus H. Milne Edwards, 1848: 61.
Dardanus megistos.—Rathbun in Stimpson, 1907: 205 (footnote).—Humes, 1981: 7, 11.
Pagurus megistos.—Fize & Serène, 1955: 158, 159, 160, text fig. 24, pl. 4A.

Material examined. BANDA Stn 22, 1♀ ov (NIOJ). PULAU MARSEGU, western Seram, coll. A.G. Humes, 1♀ ov (NIOJ). SAPARUA Stn 2, 1♀ (NIOJ).

Colour in life. Not recorded. Several authors, including Fize & Serène (1955: 165), have provided information on live colouration of this species, and several photographs in colour have been published.

Remarks. The specimens from Banda and Saparua were found at night, on rock in 0–4 m of water. The crab collected by A.G. Humes was the host of copepods (Humes, 1981).

Distribution. East coast of Africa to Hawaiian Islands and Tuamotu Archipelago.

Dardanus pedunculatus (Herbst)

- Cancer pedunculatus* Herbst, 1804: 25, pl. 61 fig. 3.
Pagurus asper De Haan, 1849: 208, pl. 49 fig. 4.—Alcock, 1905b: 90, pl. 9 fig. 5.
Pagurus sigmoidalis Zehntner, 1894: 192, pl. 8 fig. 19a,b.
Dardanus haanii Rathbun, 1902: 34.
Neopagurus horai Kamalaveni, 1950: 83, figs 2a–c, 3.
Pagurus haani.—Fize & Serène, 1955: 158, 159, 207, text figs 32, 33, pl. 4.
Dardanus pedunculatus.—Lewinsohn, 1969: 29, pl. 1 fig. 3.

Material examined. SERAM Stn 2, 1♂ (NIOJ). SAPARUA Stn 1, 1♀ juv (NIOJ).

Colour in life. Carapace mottled tan and cream; shield with median reddish brown spot near anterior margin. Ground colour of ocular peduncles white; broad red band proximally, incomplete broad red band just next to black cornea. Antennular peduncles transparent except for red stripe laterally and mesially; flagellum pale red. Antennal flagella transparent. Ground colour of chelipeds cream to light brown, with mottling of darker brown on carpus and inner side of palm. Second and third pereopods uniform orange brown.

Remarks. The specimen from Seram was taken in 1–3 m and, like *Dardanus gemmatus*, carried two species of anemones on its shell. Anemones were not associated with the individual from Saparua, which was collected in 6–8 m on a sandy bottom grading onto coral-covered rock.

Observations on the association of *Dardanus pedunculatus* with anemones were made by Cowles (1919) and by Ross (1975).

Distribution. East coast of Africa to Hawaiian Islands.

***Dardanus setifer* (H. Milne Edwards)**

Pagurus setifer H. Milne Edwards, 1836: 274.—Alcock, 1905b: 83, pl. 8 fig. 3.—Fize & Serène, 1955: 158, 159, 182, text figs 27, 28, pl. 5 figs 4–8.

Dardanus setifer.—Gordan, 1956: 316.

Material examined. ARAFURA Stn 6, 1♂ juv (AHF).

Colour in life. Carapace mottled red and white. Ocular peduncles uniform pinkish orange; cornea silvery gray. Antennules and antennae uniform pinkish orange. Chelae mottled red and white with black tips on fingers. Pereopods 2 and 3 mottled red and white with black claws, and with distinct bands of darker red on carpus and propodus.

Remarks. Collected in 49 m on an unknown substrate.

Distribution. South Africa, Madagascar, Mauritius, Pakistan, India, Sri Lanka, Vietnam, Hong Kong and Australia. Not recorded previously from Torres Strait.

***Dardanus woodmasoni* (Alcock)**

Pagurus wood-masoni Alcock, 1905a: 831; 1905b: 85, pl. 9 fig. 3.—Fize & Serène, 1955: 158, 159, 195, text fig. 30, pl. 6 figs 1–4.

Dardanus wood-masoni.—Gordan, 1956: 316.

Material examined. BANDA Stn 10, 1♂ (NIOJ).

Colour in life. Carapace mottled in various shades of gray brown; 3 dark brown blotches on anterior part of shield. Ocular peduncles solid gray brown, cornea silver. Antennules uniform transparent gray brown. Antennal flagella uniform transparent brown. Chelipeds different shades of brown with white spines and setae. Pereopods 2 and 3 mottled brown and white, with darker brown, indistinct dorsomedian band on merus, carpus and propodus; spines and setae white.

Remarks. This specimen was taken from a bottom of sandy mud in 2 m of water.

Distribution. Red Sea, Maldives and Andaman Islands, Vietnam, Philippines, Ryukyu Islands and Marshall Islands and herein recorded from Indonesia.

Diogenes* Dana**Diogenes avarus* Heller**

Diogenes avarus Heller, 1865: 83, pl. 7 fig. 2.—Alcock, 1905b: 61, 68, pl. 6 figs 6, 6a.—Forest, 1957: 524, figs 1–4.—Lewinsohn, 1969: 37, fig. 4.

Material examined. BANDA Stn 18, 2♂, 6♀ ov, 11 juv (NIOJ, AM P37740).

Colour in life. Carapace rather uniform dark brown. Ocular peduncles uniform light brown; or brown with broad, oblique white band medially; cornea golden. Proximal segment of antennular peduncles dark brown; distal segment with brown

chromatophores on white. Antennal flagella banded brown and white. Merus and carpus of large cheliped solid light brown, chela white; small cheliped solid light brown. Merus of pereopods 2 and 3 white, with 2 brown bands; carpus light brown with white band distally; propodus white medially, otherwise dark brown proximally and light brown distally; dactyl dark brown proximally and white distally.

Remarks. The specimens were found in 0–2 m on a fine sand and gravel beach. All of them are very small, and most, including a male with fully developed gonopores (SL 0.8 mm) and six ovigerous females (SL 0.5–0.8 mm), show juvenile characters. One somewhat larger male (SL 1.5 mm) has the elongate left cheliped that is characteristic of males of this species.

In the field, these hermits were observed making long leaps backward and running about very rapidly.

Distribution. Indian Ocean, from Red Sea and east coast of Africa to Mergui Archipelago; Malay Peninsula, Vietnam, Philippine Islands and northeast coast of Australia. Now reported from Indonesia for the first time.

***Diogenes jousseaumei* (Bouvier)**

Troglopagurus jousseaumei Bouvier, 1897: 231, fig. 6.

Troglopagurus jousseaumii.—Alcock, 1905b: 75, pl. 5 fig. 6.

Diogenes jousseaumei.—Forest, 1952a: 9 et seq., fig. 15.

Material examined. ARAFURA Stn 3, 1♂, 1♀ (AHF); Stn 8, 1♂ (AM P37792); Stn 11, 1♂, 2♀ (1 ov) (AM P37736); Stn 12, 1♀ ov (AM P37794); Stn 13, 1♀ ov (AHF); Stn 15, 1♂ (AHF).

Colour in life. Carapace mottled brown and white. Ocular peduncles white with dorsal brown stripe; cornea almost silver. Antennae transparent. Chelipeds covered with dense, whitish gray setae. Pereopods 2 and 3 banded alternately brown and white; with dense, whitish gray setae.

Remarks. The specimens were collected on unknown substrates in 49–99 m. In a single specimen, a male from Station 3, the rostriform process is obsolescent and scarcely visible. In the rest of the material it is very small but distinct, as depicted by Forest (1952a: fig. 15). The fixed finger and lower margin of the palm of the left cheliped form a nearly straight line in our specimens, instead of a curve with the fingers deflexed as reported by Bouvier and Alcock.

Distribution. Persian Gulf, Gulf of Oman, Red Sea, Gulf of Aden, India, Sri Lanka and Queensland. Not previously reported from Torres Strait and the Arafura Sea.

***Diogenes rectimanus* Miers**

Diogenes rectimanus Miers, 1884: 262, pl. 27 fig. C.—Alcock, 1905b: 61, 71, pl. 6 fig. 8, pl. 7 fig. 2.

Material examined. ARAFURA Stn 13, 1♀ ov (AM P37785).

Colour in life. Not noted.

Remarks. The specimen was collected in 64 m. There is a second spine near the apex of the rostriform process, giving it a bifid appearance; the spines on the lower margin of the palm of the left chela are reduced, taking the form of well-developed granules with rounded tips; and the propodus and dactyl of pereopods 2 and 3 are considerably more slender than those illustrated by Alcock. Otherwise, the specimen agrees well with the published descriptions and figures.

Distribution. Persian Gulf, Gulf of Aden, India, Sri Lanka, Malay Peninsula, Arafura Sea and Torres Strait (the type locality).

Diogenes serenei Forest

Diogenes serenei Forest, 1957: 530, figs 12–15.—Ball & Haig, 1972: 91.

Material examined. BANDA Stn 10, 2♂, 1♀ (NIOJ, AM P37754); Stn 24a, 1♂ (NIOJ).

Colour in life. Carapace mottled brown and white; shield with submedian dark brown spot near each lateral margin. Ocular peduncles with light brown mottling proximally, white distally, with dark brown ring in white area; cornea silver. Antennular peduncles with transparent background; basal segment with subdistal dark brown band, terminal segment with similar band distally. Antennal peduncles white, terminal segment with subdistal brown band; flagellum transparent brown. Chelipeds mottled black, white and brown. Pereopods 2 and 3 mottled brown and white; submedian black spot on dorsal margin of merus and carpus.

Remarks. The specimens came from areas of sandy mud and rocks in 0–3 m.

Distribution. Gulf of Iran, Vietnam and eastern New Guinea and herein recorded from Indonesia.

Diogenes viridis n.sp.

Fig. 3

Material examined. HOLOTYPE: BANDA Stn 20, 1♂ SL 1.8 mm (NIOJ A.019). PARATYPE: BANDA Stn 21, 1♀ SL 1.3 mm (NIOJ A.011).

Description. Shield flattened, approximately as broad as long; anterior margin between rostrum and lateral projections concave; posterior margin truncate; anterolateral margins strongly convex, with row of spines and with long setae; anterolateral portion of dorsal surface with numerous spines (most of them poorly developed in paratype); well-developed submarginal spine at anterolateral angle. Rostrum short, broad, obtusely triangular. Lateral projections exceeding rostrum, broad, triangular, with small terminal spine.

Ocular peduncles about equal to length of shield; sparsely setose. Ocular acicles with mesial margin somewhat concave, lateral margin sloping; terminating in 2 or 3 spines and with long setae distally; well separated basally. Intercalary rostral process rounded triangular, with slender spine at tip; shorter than ocular acicles; no spine on ventral surface.

Antennular peduncles stout, short, barely reaching distal half of ocular peduncles. Ultimate and penultimate segments unarmed; basal segment with spine at ventrolateral distal angle.

Antennal peduncles short, barely reaching distal half of ocular peduncles; with supernumerary segmentation. Fifth segment slender, unarmed, with long setae. Fourth and third segments unarmed and with tufts of setae. Second segment with strong spine at dorsolateral distal angle; lateral margin unarmed; dorsomesial margin with 2 well-developed spines. First segment slightly produced at dorsolateral distal angle. Antennal acicle short, slightly exceeding distal end of fourth peduncular segment; terminating in strong spine; lateral margin with 2 strong spines, mesial margin with 2 or 3 spines; margins with long setae. Antennal flagella rather short, composed of 10 articles; with long setae.

Maxillule with endopodite lacking external lobe. First maxilliped with flagellum of exopodite biarticulate. Second maxilliped with exopodite exceeding base of dactyl of endopodite. Third maxilliped with ischium unarmed (lacking crista dentata); basis with 2 well-developed spines.

Left cheliped missing in paratype. Left cheliped of holotype with dactyl approximately as long as upper margin of palm; rather strongly curved; cutting edge with well-developed calcareous teeth; terminating in small calcareous claw, latter hidden under tip of fixed finger; outer surface finely granulate, with submedian longitudinal row of spinules and with long setae; upper margin with row of strong spines decreasing in size distally; inner surface smooth. Fixed finger with small calcareous tubercles on cutting edge; terminating in small calcareous claw; outer surface with irregular rows of spinules or pointed granules and with long setae; lower margin curved, with row of spines; inner surface nearly smooth. Palm flattened; upper margin about as long as carpus, somewhat cristate, with row of 8 strong spines and with long setae; outer surface with scattered, minute granules, and with small, closely set spines near upper and lower margins; lower margin nearly straight, with long setae and with row of strong spines, latter becoming smaller proximally and distally where they pass into row on lower margin of fixed finger; inner surface smooth. Carpus slightly longer than merus; upper margin with 4 spines, proximal one poorly developed, and with scattered setae; outer surface with scattered spinules or pointed granules, outer distal margin with row of spinules; inner surface with large spine at upper

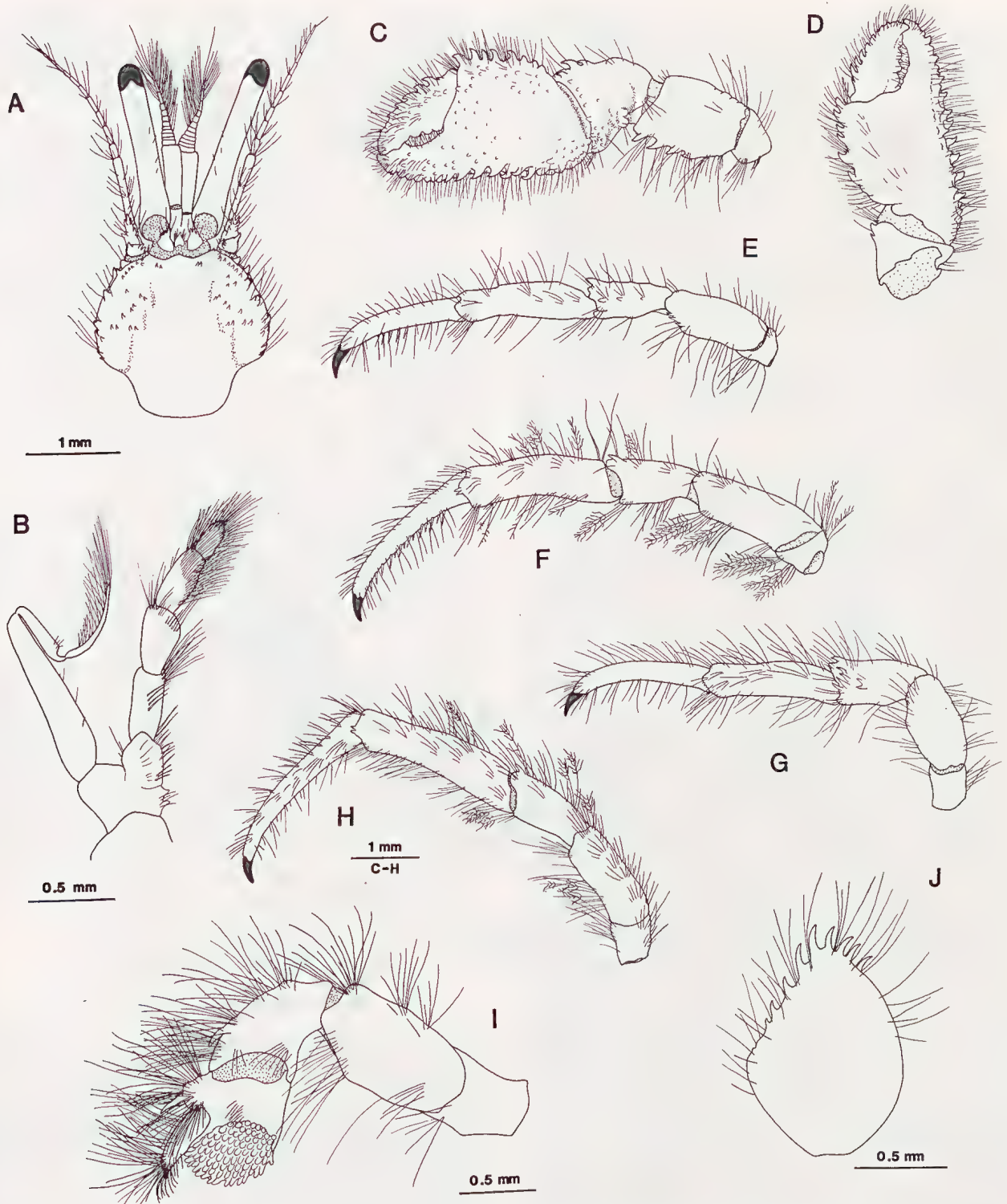


Fig.3. *Diogenes viridis* n.sp. [Holotype ♂, Banda Stn 20]. **A**, shield and anterior appendages; **B**, mxp 3 (left, internal view); **C**, left cheliped (outer view); **D**, left chela (inner view); **E**, left P 2 (lateral view); **F**, right P 2 (mesial view); **G**, left P 3 (lateral view); **H**, right P 3 (mesial view); **I**, left P 4 (lateral view); **J**, telson.

distal corner. Merus with outer surface minutely granulate; upper margin obscurely crenulate in proximal half; lower margin with 4 strong spines; margins and inner surface with long setae.

Right cheliped missing in both specimens.

Left second pereopod with dactyl approximately as long as propodus; terminating in strongly curved corneous claw; all surfaces with long and short setae. Propodus nearly twice length of carpus; mesial surface with 2 small spines on median part of distal margin; small spine at ventrodistal angle; all surfaces with long and short setae. Carpus $\frac{2}{3}$ length of merus; dorsal margin with 2 strong spines distally; lateral surface with 3 spines in median longitudinal row, most proximal one very small; long and short setae most abundant on dorsal margin and lateral surface. Merus with lateral surface armed with row of 3 small spines ventrodistally; dorsal and ventral margins with long setae.

Right second pereopod considerably longer than left. Dactyl approximately as long as propodus. Propodus about twice length of carpus; lateral and mesial surfaces each with 2 small spines on median part of distal margin. Carpus about $\frac{3}{4}$ length of merus; dorsal margin with strong spine distally; lateral surface with median longitudinal row composed of transverse group of 3 well-developed spines near distal margin, 1 well-developed spine on middle third of segment, very small spine on proximal third. Merus armed as in left pereopod 2. Setation as in left pereopod 2.

Left third pereopod with proportional lengths of first 4 segments approximately same as in left pereopod 2. Dactyl terminating in strongly curved corneous claw. Propodus with lateral surface bearing 3 minute spines on ventral part of distal margin; mesial surface with small spine on median part, 2 or 3 minute spines or pointed granules on ventral part of distal margin. Carpus with dorsal margin armed with strong spine distally; lateral surface with distal transverse row of 4 strong spines, pair of smaller, more proximal spines on median part of segment. Merus with lateral surface armed with 2 strong spines ventrodistally. Setation as in left pereopod 2. Right third pereopod considerably longer than left. Proportional lengths of first 4 segments approximately same as in right pereopod 2. Dactyl as in right pereopod 2. Propodus armed as in right pereopod 2. Carpus with dorsal margin armed with strong spine distally; lateral surface with distal transverse row of 3 strong spines, and more proximal, much smaller spine on median part of segment. Merus armed as in right pereopod 2. Setation as in left pereopod 2.

Fourth pereopods with dactyl terminating in small corneous claw. Propodus with very prominent spine on dorsal margin; rasp well developed. Carpus with large curved spine on dorsal margin.

Sternal plastron very broad; all 5 pairs of pereopods well separated at their bases.

Uropods asymmetrical. Telson considerably longer than broad, without transverse median constriction; terminal margin entire (not bilobed); terminal and lateral margins armed with 9 spines interspersed with long setae.

Colour in life. Carapace white, with 2 green spots just behind shield. Ocular peduncles uniform light pink. Antennules uniform white. Antennae solid green except for white band at distal end of peduncle. Left cheliped with merus green proximally, white distally; carpus and chela white. Pereopods 2 and 3 with merus and carpus green, these segments sometimes with small, dorsodistal white patch; propodus green except for broad white band distally; dactyl white.

Pale but distinct green tint persisting on pereopods 2 and 3 after several years' preservation in alcohol.

Remarks. The holotype was collected on sandy mud grading onto coral, in 0–4 m; the paratype on cobbles and large boulders in about 2 m.

Diogenes viridis belongs to a small group of Indo-West Pacific species in which the antennal peduncles are slender and shorter than the ocular peduncles. This group includes *D. gardineri* Alcock, *D. serenei* Forest, and *D. leptocerus* Forest (Forest, 1957); *D. pallescens* Whitelegge (Ball & Haig, 1972); *D. capricorneus* Grant & McCulloch (Grant & McCulloch, 1906); and a *Diogenes* from the coast of New South Wales which is probably to be identified with *D. senex* Heller. In all those species the carapace shield is longer than broad, with its lateral margins straight instead of strongly convex, the antennular peduncles are slender and much longer in relation to the ocular peduncles than they are in *D. viridis*, and the sternal plastron is not exceptionally broadened.

Etymology. From Latin *viridis*, green, for the distinctive colouration of the species.

Paguristes Stimpson

Paguristes kuekenthali De Man

Figs 4, 5

Paguristes küekenthali De Man, 1902: 733, pl. 24 figs 43, 43a–f.

Material examined. BANDA Stn 9, 1♂, 3♀ (AHF); Stn 11, 1♂ (AHF); Stn 12, 1♂, 3♀ (NIOJ); Stn 19, 1♀ (AM P37749); Stn 23b, 2♂ (AM P37734). SERAM Stn 2, 1♀ (NIOJ). SAPARUA Stn 3, 1♀ (NIOJ).

Description. Shield longer than broad; anterior half of dorsal surface and margins with numerous small spines. Rostrum long, considerably exceeding lateral projections; broad at base and terminating acutely. Ocular peduncles long, about $\frac{7}{10}$ length of shield; relatively stout. Ocular acicles widely separated basally, terminating in 2–4 spines. Antennular and antennal peduncles slightly shorter than ocular peduncles. Antennal flagella of moderate length, slightly over-reaching tips of chelipeds but shorter

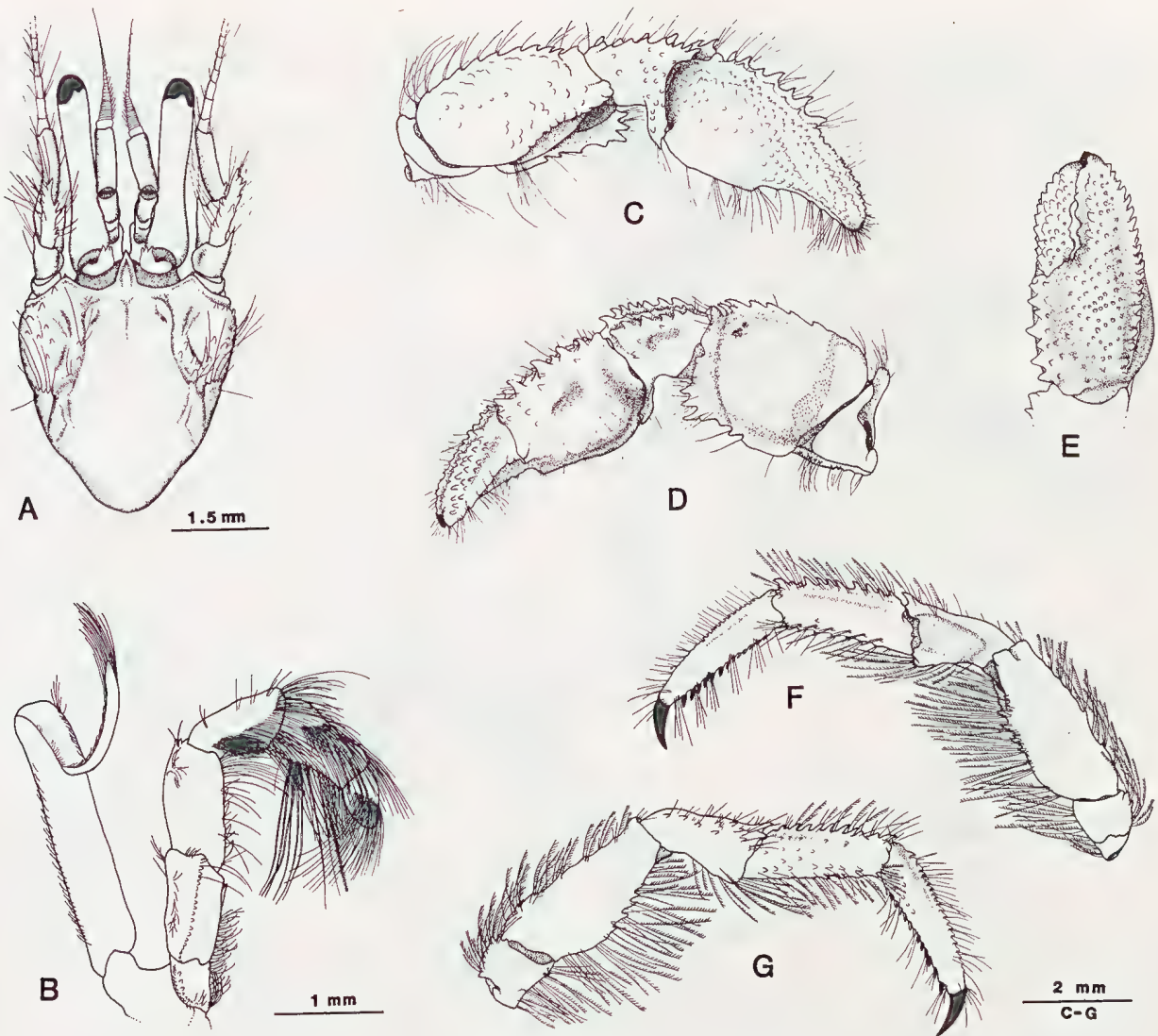


Fig.4. *Paguristes kuekenthali* De Man. [A, ♂, Banda Stn 23b; B–G, ♂, Banda Stn 11]. A, shield and anterior appendages; B, mxp 3 (left, internal view); C, right cheliped (lateral view); D, right cheliped (mesial view); E, right chela (dorsal view); F, left P 2 (lateral view); G, left P 2 (mesial view).

than carapace; with setae of varying lengths, longest ones about equal in length to 4 articles.

Chelipeds with tufts of long setae, especially on mesial margins and ventral faces. Chela with pointed granules over dorsal surface; dorsolateral margin of palm and fixed finger with row of about 16–24 small spines; dorsomesial margin of palm with 4 or 5 strong spines. Carpus with dorsal surface nearly smooth except for few rounded granules; dorsolateral margin with 5 or 6 spines; dorsomesial margin with 4 or 5 strong spines. Merus with row of strong spines on dorsal and ventromesial margins. Second and third pereopods relatively slender, with fringe of long setae on dorsal and ventral margins of all segments. Dactyl with row of small spines or pointed granules along dorsal margin; ventral margin with row of corneous spines. Propodus with row of spines on dorsal margin of pereopod 2, this margin unarmed or with row of

minute spines in pereopod 3. Carpus with row of spines, dorsodistal one strongest.

Male paired first pleopods with short row of rather widely spaced, hooked spines on distal margin of inferior lamella. Females with gonopore on coxa of left pereopod 3 only; brood pouch absent. Female paired first pleopods slender, with very long plumose setae on margins of terminal portion.

Telson with few minute spines on terminal margin of posterior lobes.

Colour in life. Shield uniform white or pale orange. Ocular peduncles and corneas solid bright orange. Antennules uniform orange, flagellum transparent. Antennal flagella alternately transparent and red or purple. Chelipeds bright orange; merus with red or dark purple spot on lateral and ventral faces, 2 spots on mesial face; carpus and chela each with similar marking on dorsal, lateral and mesial faces.

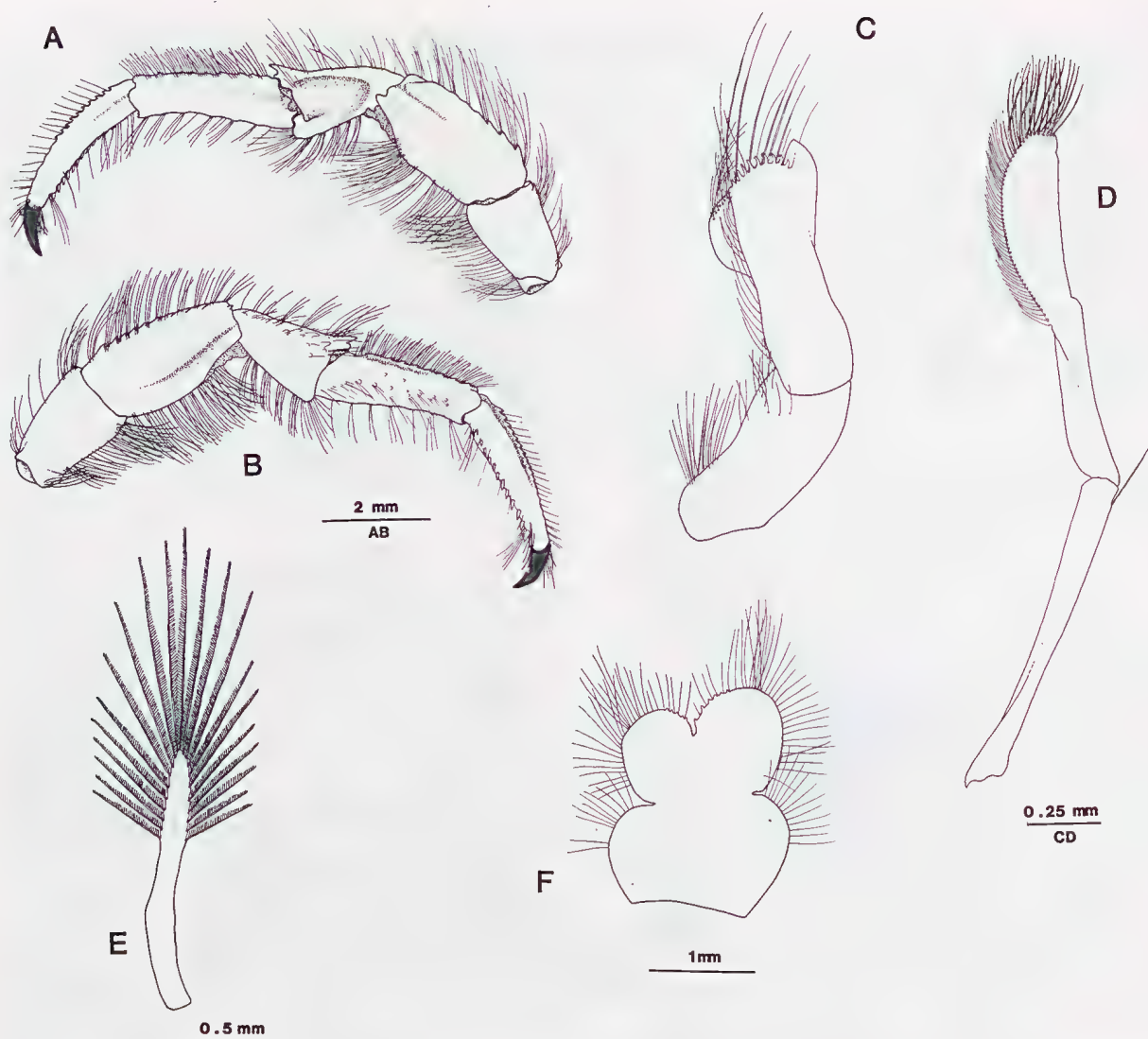


Fig.5. *Paguristes kuekenthali* De Man. [A,B,F, ♂, Banda Stn 11; C,D, ♂, Banda Stn 23b; E, ♀, Banda Stn 12]. A, left P 3 (lateral view); B, left P 3 (mesial view); C, male pl 1 (left); D, male pl 2 (left); E, female pl 1; F, telson.

Pereopods 2 and 3 bright orange, with lateral red patch on mērus and carpus.

Remarks. Specimens were taken from rock and coral bottoms in depths of 0–20 m.

Through the courtesy of Dr Michael Türkay, J. Haig was able to borrow the holotype and only known specimen of *Paguristes kuekenthali*, an ovigerous female (SL 3.0 mm) in the collections of the Natur-Museum Senckenberg, Frankfurt am Main (SMF 8560). Examination of this specimen confirmed the identity of our material with De Man's species. Our series of individuals of both sexes and different sizes (males SL 2.2–4.6 mm, females 2.2–4.7 mm) has made it possible to define the species more precisely.

De Man (1902) seems to have been the first to record an Indo-West Pacific species of *Paguristes*

with the right gonopore lacking in females. He noted this phenomenon when describing *P. kuekenthali*, but believed it to be an abnormality. Subsequently, unpaired female gonopores have been reported in *P. jousseaumei* Bouvier, *P. perspicax* Nobili, and *P. abbreviatus* Dechancé (Dechancé, 1963), and in *P. monoporus* Morgan (Morgan, 1987). They are now noted in *P. hians* Henderson (see below under *P. monoporus*). The type locality of *Paguristes kuekenthali* is Ternate in Maluku. The material collected by the *Alpha Helix* slightly extends the known range to Banda, Seram and Saparua in the same group of islands. While work on this report was in progress, a female *P. kuekenthali* (SL 4.5 mm) from Efate Island, New Hebrides (now Vanuatu) was donated to the crustacean collections of the Allan Hancock Foundation. This specimen, which was

taken by Alex Kerstitch in 10 m of water from rubble on a coral reef, establishes a further extension of range eastward.

Distribution. Maluku, Indonesia; Vanuatu.

Paguristes monoporus Morgan

Paguristes hians.—Grant & McCulloch, 1906: 33 (in part).—McCulloch, 1913: 346. [Not *Paguristes hians* Henderson.]

Paguristes monoporus Morgan, 1987: 379, figs 1–3.

Material examined. BANDA Stn 5b, 1♂, 1♀ (AM P37796); Stn 9, 1♀ (NIOJ); Stn 12, 1♂ (AM P37791); Stn 13, 1♂ (NIOJ); Stn 14, 1♂ (NIOJ); Stn 19, 1♀ (NIOJ); Stn 23b, 1♂, 1♀ ov (AHF); Stn 24a, 1♂ (AHF). SERAM Stn 2, 2♀ (NIOJ).

Colour in life. Carapace mottled white and salmon or brown. Ocular peduncles longitudinally striped purple and white or purple and orange, stripes continuing onto cornea. Antennular peduncles with basal segment brown or purple, terminal segment blue or green; flagellum orange. Antennal flagella alternately banded brown and transparent. Chelipeds with merus mottled dark brownish purple through white; carpus and chela fairly uniform orange tan on white. Pereopods 2 and 3 with orange-tan or brown longitudinal stripes on white background; merus and carpus sometimes mottled brown and white. Setation white.

Remarks. Most specimens were collected in depths of less than 5 m, generally on corals. There was no clear correlation with exposure.

The female specimen from Banda Station 9 was infected by a rhizocephalan. One specimen from Seram Station 2 was parasitised by a branchial bopyrid, *?Bopyrissa* sp., and by a pair of abdominal bopyrids, *Parathelges ?whiteleggei* Nierstrasz & Brender à Brandis. The same crab was further burdened with a rhizocephalan attached to the abdomen.

Paguristes monoporus is distinguished by the absence in males of the left gonopore and left second pleopod, together with extreme reduction in size of the left first pleopod. Because the antennal flagella are shorter than the carapace, the antennular peduncles are as long as or slightly shorter than the ocular peduncles, and the chelae are heavily setose with an hiatus between the dactyl and the fixed finger, it superficially resembles *Paguristes hians* Henderson. The latter species, which has been reported from several localities in the Indo-West Pacific, differs from *P. monoporus* by the presence of equal-sized first pleopods and paired gonopores in males, the absence of both male second pleopods, and the presence in females of a large brood pouch; as in Morgan's species, females of *P. hians* have a gonopore on the left side only (unpublished observations by J. Haig).

Reporting on a collection of crustaceans made in Queensland in 1904, Grant & McCulloch (1906: 33)

noted that *Paguristes hians* is "...fairly common in depths of 17–20 fathoms off Mast Head Island". J. Haig has examined a sample of three specimens labelled *Paguristes hians* in the collections of the Australian Museum (AM G5732). The accompanying data (Masthead Island, F.E. Grant, Feb. 1907, 17 fathoms) show that these specimens were presented to the Museum by Grant in 1907 and that they are at least part of the material identified and reported by Grant & McCulloch (1906) as *P. hians*. A female *Paguristes* (SL 1.8 mm, AM P37790) in the sample could not be identified and probably belongs to an undescribed species. It superficially resembles *P. hians* but differs from the latter in having long antennal flagella with very long setae on their ventral margin and paired gonopores on the coxae of the third pereopods, and in lacking a brood pouch. The other two specimens (♂ SL 2.8 mm, ♀ SL 2.1 mm) proved to be *P. monoporus*. At present there is no evidence that *P. hians* occurs in Australian waters.

Distribution. Northern Territory, Australia and herein recorded from Maluku and Capricorn Group, Queensland.

Paguristes runyanae n.sp.

Figs 6, 7

Material examined. HOLOTYPE: BANDA Stn 1, ♂ SL 5.8 mm (NIOJ A.020). PARATYPES: BANDA Stn 1, 1♂ SL 4.8 mm (AHF 756); Stn 2, 1♀ ov SL 4.7 mm (NIOJ A.007).

Description. Shield considerably longer than broad; anterior margin between rostrum and lateral projections concave; posterior margin truncate; dorsolateral surfaces and margins with small spines and long plumose setae. Rostrum long, slender, considerably exceeding lateral projections; terminating acutely. Lateral projections broadly triangular, with acute spinule at tip.

Ocular peduncles slender, very long, nearly or quite equalling length of shield; slightly inflated basally; dorsal surface with few long setae proximally. Ocular acicles with mesial margin straight or rather uneven; terminating in acute spine; widely separated basally.

Antennular peduncles $\frac{2}{3}$ to $\frac{3}{4}$ length of ocular peduncles. Ultimate and penultimate segments unarmed; basal segment with small spine at ventromesial distal angle and prominent spine on lateral face.

Antennal peduncles reaching distal half to distal third of ocular peduncles; with supernumerary segmentation. Fifth segment unarmed. Fourth segment sometimes with small spine on dorsodistal margin. Third segment with ventromesial distal angle produced, terminating in strong acute spine. Second segment with dorsolateral distal angle produced, terminating in acute single or bifid spine; dorsomesial distal angle with small spine; lateral and

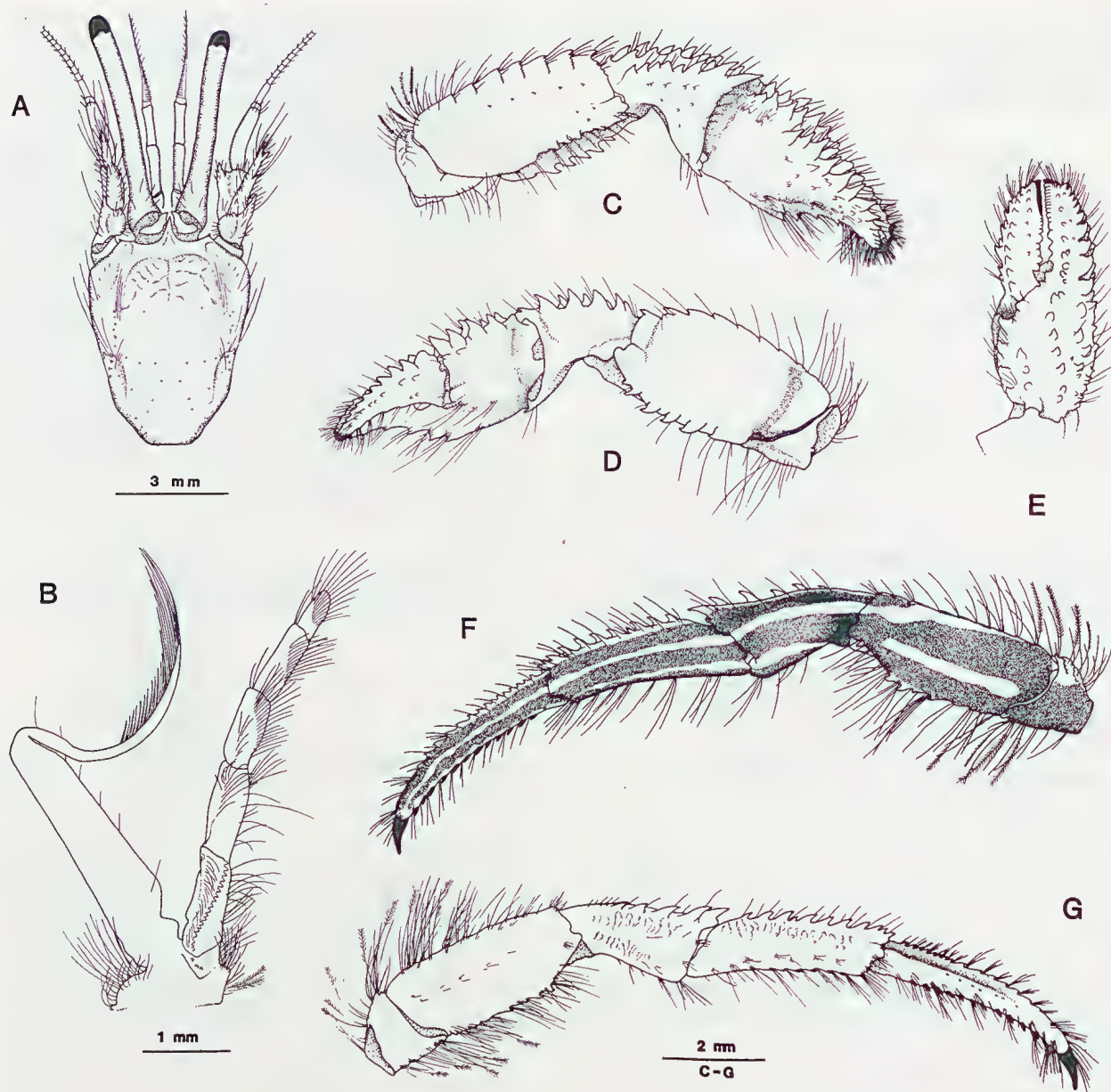


Fig.6. *Paguristes runyanae* n.sp. [A, holotype ♂, Banda Stn 1; B–G, ♂, Banda Stn 1]. A, shield and anterior appendages; B, mxp 3 (left, internal view); C, right cheliped (lateral view); D, right cheliped (mesial view); E, right chela (dorsal view); F, left P 2 (lateral view); G, left P 2 (mesial view).

mesial margins unarmed; lateral margin with long setae. First segment unarmed. Antennal acicle reaching proximal half to distal fourth of ultimate peduncular segment; terminating in bifid spine; lateral margin with 1–3 spines, mesial margin with 2–4; with long setae. Antennal flagella long, over-reaching tips of chelipeds and longer than carapace; each article with several short setae.

Third maxillipeds with basis and ischium distinctly separate; basis with 3 or 4 small spines; ischium with crista dentata evenly developed, ventral margin with small spine distally; merus with 3–5 prominent spines on ventral margin; carpus with

small spine on dorsodistal margin, sometimes 1 on ventrodistal margin.

Chelipeds subequal, left slightly more slender than right. Dactyl about $\frac{1}{3}$ longer than palm; cutting edge with calcareous teeth proximally, corneous teeth distally; terminating in small corneous claw; dorsal surface with row of small corneous-tipped spines or tubercles near cutting edge, dorsomesial margin with row of well-developed, corneous-tipped spines decreasing in size distally; mesial face with row of small corneous-tipped spines, and with scattered corneous-tipped tubercles near ventral margin; ventral face nearly smooth; all surfaces with tufts of

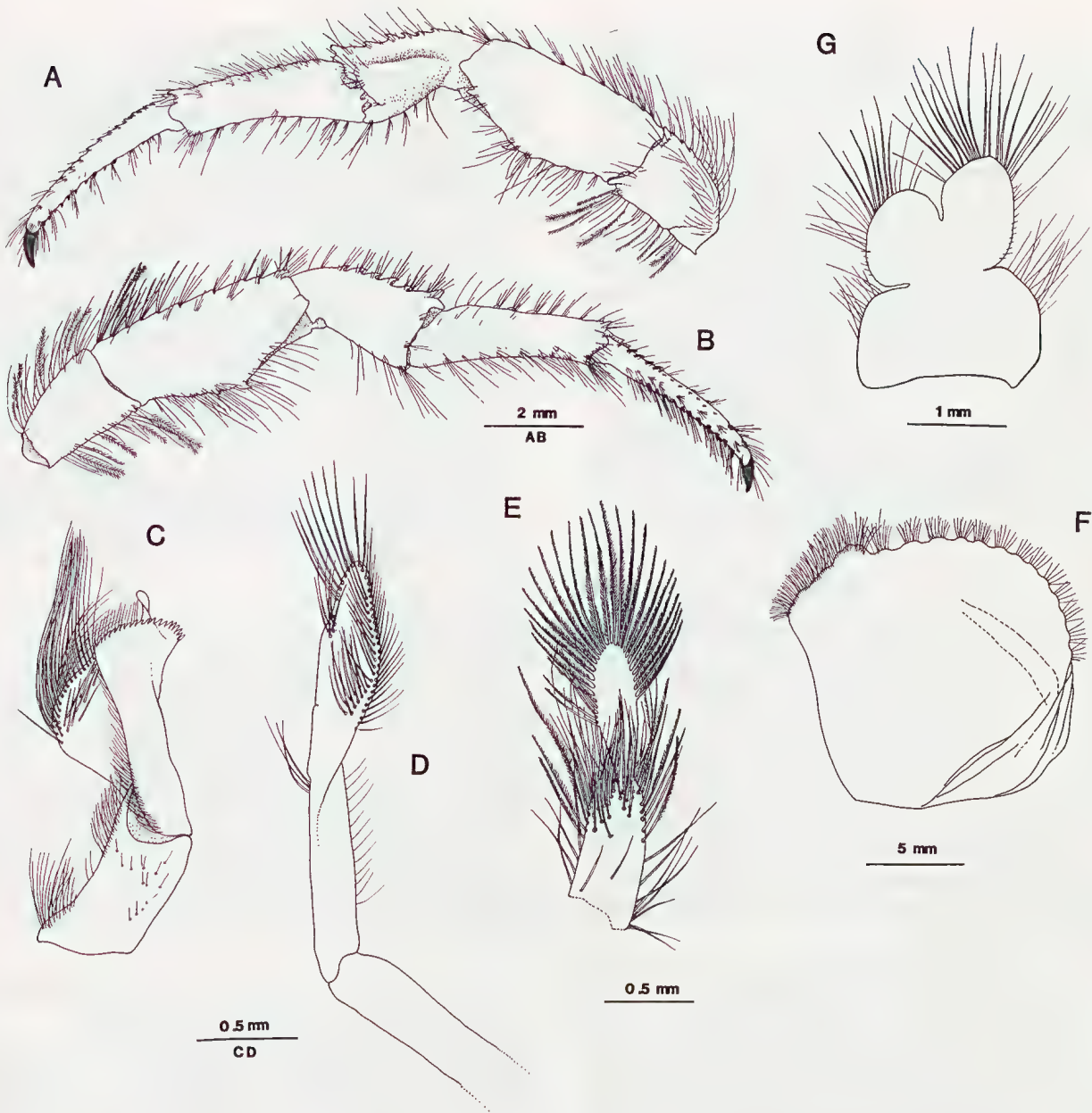


Fig. 7. *Paguristes runyanae* n.sp. [A, B, ♂, Banda Stn 1; C, D, holotype ♂, Banda Stn 1; E–G, ♀, Banda Stn 2]. A, left P 3 (lateral view); B, left P 3 (mesial view); C, male pl 1 (left); D, male pl 2 (right); E, female pl 1; F, brood pouch; G, telson.

setae. Fixed finger slightly broader than dactyl; cutting edge with calcareous teeth, forming narrow hiatus with dactyl proximally; terminating in corneous claw; dorsal surface with row of conical, corneous-tipped spines near cutting edge; lateral face with row of small corneous-tipped spines near dorsal and another near ventral margin; ventral face with tufts of setae, these more thickly set distally. Palm about $\frac{2}{3}$ length of carpus; dorsomesial margin with 4 strong, conical, corneous-tipped spines; dorsal surface with irregular, widely spaced longitudinal rows of well-developed conical spines, and with scattered short setae; mesial face smooth except for a few spinulose tubercles near dorsomesial spine row

and along distal margin; dorsolateral margin with row of well-developed spines, these continuing to tip of fixed finger; lateral face with irregular row of small spines or spine-tipped tubercles, these continuing onto fixed finger; ventral surface with few spinulose tubercles and tufts of long setae. Carpus $\frac{3}{5}$ to $\frac{2}{3}$ length of merus; dorsomesial margin with 4 to 6 strong, corneous-tipped spines; dorsal surface with submedian row of small corneous-tipped spines; dorsolateral margin with row of moderately strong spines; mesial and ventral faces nearly smooth; lateral face with scattered corneous-tipped tubercles. Merus laterally compressed, with row of crenulations on dorsal margin proximally, these becoming small

spines distally, and with long setae; lateral face faintly rugose; mesial face smooth; ventrolateral and ventromesial margins each with row of spines and with scattered setae.

Second pereopods with dactyl slender, slightly longer than propodus; terminating in strong, curved corneous claw; dorsal surface with row of small spines and with tufts of setae; lateral face nearly smooth, with few scattered tufts of setae; mesial face with median row of small corneous spinules, with broad sulcus dorsoproximally and tufts of long setae ventrally; ventral margin with row of corneous spines increasing in size distally, with tufts of long setae. Propodus slender, $1\frac{1}{3}$ to $1\frac{1}{2}$ length of carpus; dorsal surface with row of moderately strong spines and with tufts of setae; lateral face nearly smooth, with 1 or 2 small spines on ventral part of distal margin; mesial face nearly smooth, with few small spines on ventral part of distal margin, sometimes with longitudinal row of small spines near distal row, and with scattered setae; ventral surface unarmed or with row of inconspicuous spines, and with tufts of long setae. Carpus $\frac{2}{3}$ to $\frac{7}{10}$ length of merus; dorsal surface with irregular row of spines, distal 2 prominent, and with tufts of short setae; lateral face with longitudinal sulcus, otherwise smooth with few scattered setae; mesial and ventral faces smooth with scattered tufts of setae. Merus laterally compressed; dorsal margin unarmed or with row of inconspicuous spines, and with long plumose setae; lateral and mesial faces with scattered short setae; ventral margin with irregular row of spines increasing in size distally. Ischium with row of small tubercles and long plumose setae dorsally; ventral margin with small spine distally and with long plumose setae.

Third pereopods with dactyl as in second pereopods. Propodus $1\frac{1}{3}$ to $1\frac{2}{3}$ length of carpus; dorsal surface unarmed or with row of small spines, and with tufts of setae; lateral face nearly smooth, with small spines on distal margin, 1 dorsally and 2 to 4 ventrally; mesial face nearly smooth, with 3 small spines dorsodistally and 4 or 5 ventrodistally; ventral surface unarmed or with row of inconspicuous spines, and with tufts of long setae. Carpus about $\frac{4}{5}$ length of merus; dorsal surface with row of spines, distal one prominent; lateral face with longitudinal sulcus, otherwise smooth with few scattered setae; mesial and ventral faces smooth with scattered tufts of setae. Merus laterally compressed; dorsal margin with long setae; lateral face with spine ventrodistally; mesial face with scattered setae; ventral margin crenulate with 1 or 2 small spines distally, with long plumose setae. Ischium with long plumose setae on dorsal surface; ventral margin with small spine distally and with long plumose setae.

Male paired first pleopods with tuft of long bristles at superior mesial angle of basal segment, mesial margin with row of moderately long bristles distally; inferior lamella with band of long, closely set bristles

along lateral margin, distal margin with row of short, slightly curved spines; external lobe considerably exceeding inferior lamella in distal extension; internal lobe broad and much shorter than external lobe, mesial and distal margins with closely set, very long bristles. Paired second pleopods with basal segment glabrous; distal segment with marginal row of setae, endopodite with tuft of long bristles, appendix masculina with long setae on margins and exterior face.

Female gonopores paired. Paired first pleopods with long plumose setae on margins and interior face of basal segment; distal segment with row of long plumose setae on distal half of margins. Brood pouch large, subquadrate, distal margin scalloped and with tufts of setae.

Telson with posterior lobes asymmetrical, left longer than right; separated by deep median cleft; unarmed; terminal margins with long setae, lateral margins with short bristles; anterior lobes unarmed.

Colour in life. Carapace purple; shield with 3 irregularly shaped, longitudinal orange stripes (1 median, 2 sublateral), these continuing onto posterior carapace. Ocular peduncles purple, with broad white band next to black cornea; acicles orange with purple tips. Antennular peduncles purple, flagellum white. Antennal peduncles purple, distal segment with pale longitudinal stripe; flagellum purple. Chelipeds purple with bright orange longitudinal stripes, latter mostly centred over rows of spines. Pereopods 2 and 3 purple with longitudinal stripes, these mainly white but with some orange and disposed (Fig. 6F).

Remarks. The specimens were found in relatively protected subtidal areas in 0–8 m on coral.

In Alcock's (1905b) and Miyake's (1978) keys to Indian Ocean and Japanese *Paguristes*, *P. runyanae* would be placed with those species in which the antennal flagella are decidedly longer than the carapace and the antennular peduncles are shorter than (or equal to) the ocular peduncles. Of this group of species, *P. acanthomerus* Ortmann is distinguished by having a prominent spine on the ventral face of the merus of the chelipeds. In *P. seminudus* Stimpson and *P. mundus* Alcock the chelae are densely covered with spines. The chelae of *P. balanophilus* Alcock and *P. ciliatus* Heller are decorated with small, closely set tubercles: in the former species these tubercles are squamiform, in the latter acuminate and concealed by a dense tomentum. In *P. acanthomerus* and *P. balanophilus*, the only species of this group for which it has been recorded (Miyake, 1978), the live colouration is quite unlike that of *P. runyanae*.

Etymology. We are pleased to dedicate this species to our illustrator, Frances Runyan.

Trizopagurus Forest*Trizopagurus strigatus* (Herbst)

Cancer strigatus Herbst, 1804: 25, pl. 61 fig. 3.

Pagurus annulipes H. Milne Edwards, 1848: 63.

Aniculus strigatus.—Alcock, 1905b: 97, pl. 7 fig. 4.

Trizopagurus strigatus.—Forest, 1952b: 2; 1952c: 6, 19, figs 5, 14, 21.—Humes, 1981: 5, 7.

Material examined. BANDA Stn 3, 1♂ (AHF); Stn 4, 3♂, 2♀ (NIOJ); Stn 5b, 2♀ (1 ov) (NIOJ); Stn 9, 1 juv (AM P37747); Stn 19, 5♂, 3♀ (1 ov), 1 juv (AM P37753, AM P37789); Stn 20, 1♂ (NIOJ); Stn 21, 5 juv (AHF); Stn 23b, 1♀ (AHF); Stn 24b, 1♀ (AM P37793); Gunungapi, coll. A.G. Humes, 3♂, 1♀ (NIOJ, AHF). SERAM Stn 2, 3♂ (NIOJ). SAPARUA Stn 3, 1♀ (NIOJ).

Colour in life. Shield pure white. Ocular peduncles and antennules solid orange. Antennal flagella transparent. Chelipeds and pereopods 2 and 3 with alternating red and orange bands (each scute with red

distally and orange proximally).

Remarks. At Banda this species was found under all conditions of exposure; the usual depth range was 3–15 m, mostly on coral. In some areas the species was quite abundant. At Seram and Saparua it was collected in 0–5 m.

One individual from Banda Station 21 was parasitised by a rhizocephalan. The specimen from Banda Station 9 bore an abdominal bopyrid, an undescribed species of *Athelges*; the parasite, which was as large as its host, was hyperparasitised by two cabiropsid isopods, *Cabirops* sp. The specimens collected by A.G. Humes had copepods associated with them (Humes, 1981).

Distribution. Red Sea and east coast of Africa to Hawaiian and Society Islands. The type locality was "Ostindien", but the present records appear to be the first precise ones for Indonesia.

Family PAGURIDAE

Key to Genera of Paguridae Known from Maluku
in 20 Metres or Less

1. Right chela operculate, fingers opening obliquely; females with paired first pleopods *Pylopaguropsis*
 —Right chela not operculate, fingers opening horizontally; no paired pleopods in either sex 2
2. No sexual tube present in males *Pagurus*
 —Males with sexual tube on coxa of right or left pereopod 5 3
3. Males with sexual tube on coxa of right pereopod 5; dactyl of pereopod 4 with preungual process on lateral face *Catapagurus*
 —Males with sexual tube on coxa of left pereopod 5; no preungual process on dactyl of left pereopod 4 4
4. Ischium of third maxillipeds without accessory crista dentata tooth; male sexual tube terminating in tuft of setae *Anapagrides*
 —Crista dentata of third maxilliped with accessory tooth; no tuft of setae at tip of male sexual tube 5
5. Telson with terminal margin entire; eyescales subrectangular and multispinate; males with gonopore on left pereopod 5 only *Micropagurus*
 —Telson with median cleft on terminal margin; eyescales triangular or subovate, with single distal spine; male gonopores paired 6
6. Male sexual tube curved; chelipeds unequal, right much larger than left *Anapagurus*
 —Male sexual tube rolled into a spiral; chelipeds subequal, right not much larger than left *Spiropagurus*

Anapagrides de Saint Laurent-Dechancé*Anapagrides* sp.

Fig. 8

Material examined. SAPARUA Stn 3, 1♂ (NIOJ).

Colour in life. Transparent but for dark corneas and

scattered red chromatophores.

Remarks. This hermit crab (SL 2.0 mm) was taken on a cliff face of rock and coral, in 5 m or less.

De Saint Laurent-Dechancé (1966b: 262) established the genus *Anapagrides* for *Eupagurus* (*Spiropagurus*) *facetis* Melin from the Ogasawara (Bonin) Islands and for two other Indo-West Pacific

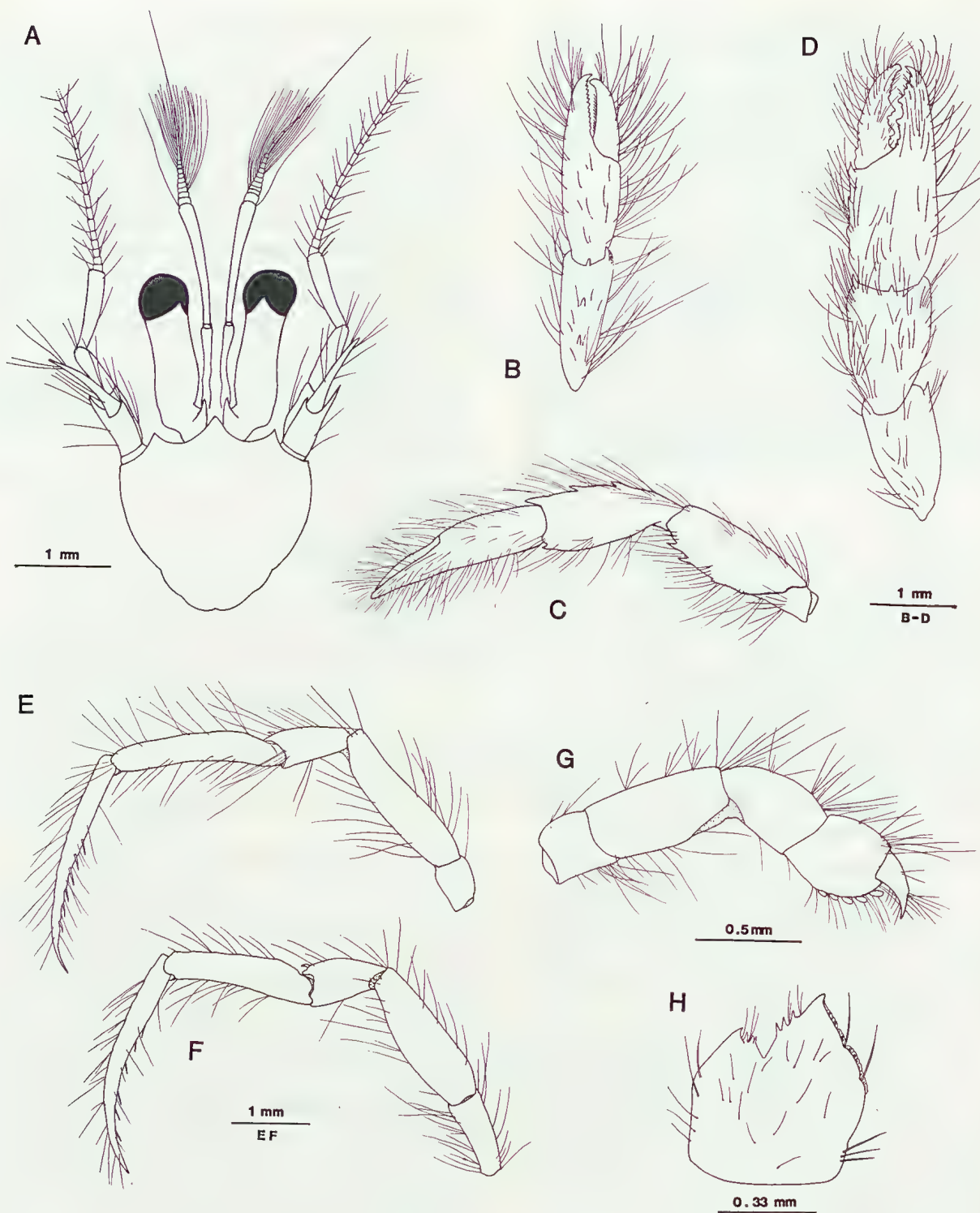


Fig.8. *Anapagrides* sp. [♂, Saparua Stn 3]. A, shield and anterior appendages; B, left chela and carpus (dorsal view); C, left cheliped (lateral view); D, right cheliped (dorsal view); E, right P 2 (mesial view); F, left P 3 (lateral view); G, right P 4 (lateral view); H, telson.

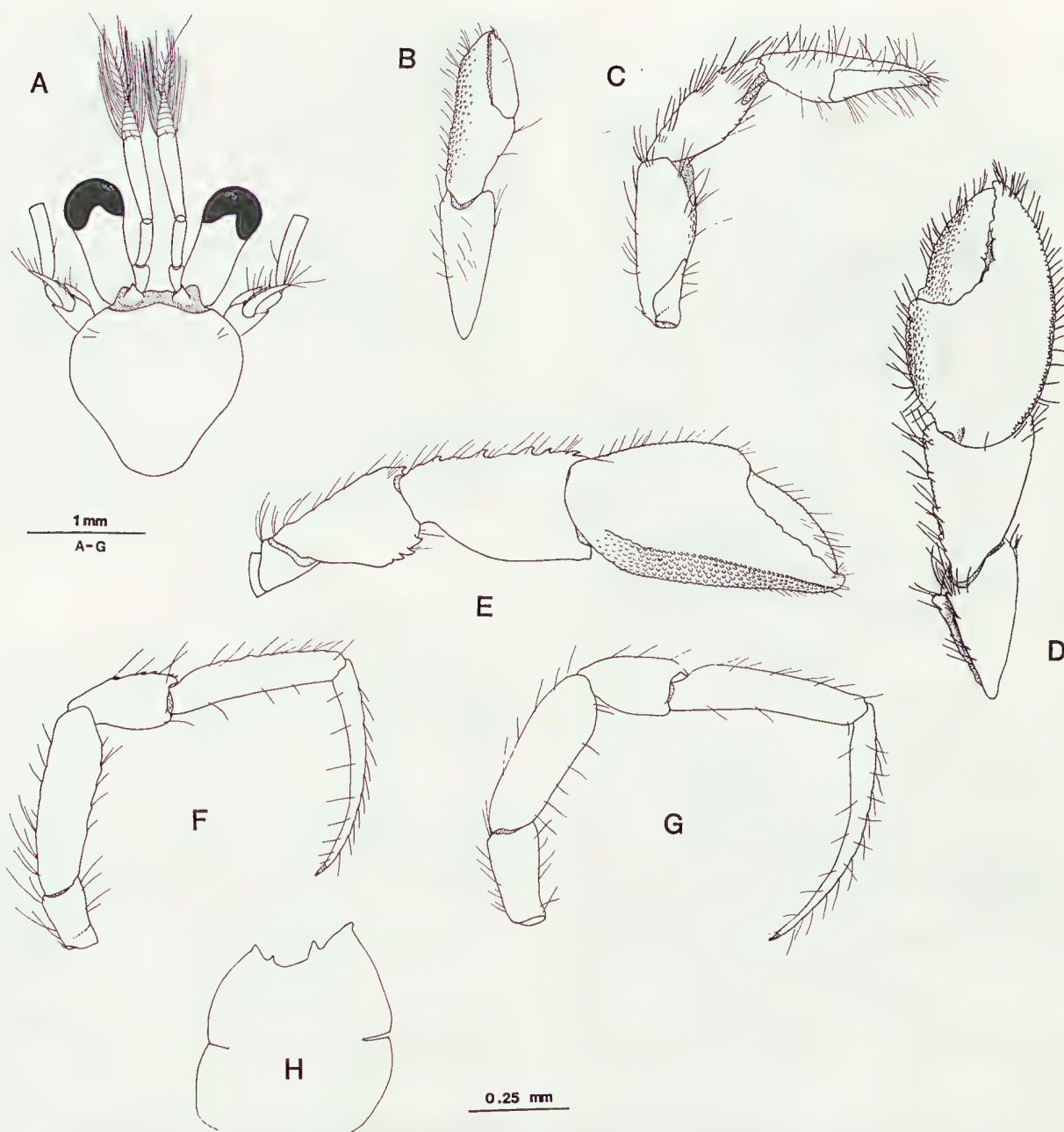


Fig.9. *Anapagurus* sp. [♂, Saparua Stn 1]. A, shield and anterior appendages; B, left chela and carpus (dorsal view); C, left cheliped (mesial view); D, right cheliped (dorsal view); E, right cheliped (dorsolateral view); F, right P 2 (lateral view); G, right P 3 (lateral view); H, telson.

species which are still undescribed. Our specimen agrees with the diagnosis of *Anapagrides* and certainly belongs in that genus, but no more can be said about its status at this time.

Anapagurus Henderson

Anapagurus sp.

Fig. 9

Material examined. SAPARUA Stn 1, 2♂, 3♀ (2 ov) (NIOJ).

Colour in life. Basically transparent except for abundant white chromatophores.

Remarks. These hermits were found on white sand in 5–7 m. They can take great leaps backwards (6–8 cm) and move very rapidly over the sand when frightened.

Not much has been published on the genus *Anapagurus* in the Indo-West Pacific, and we have been able to place these small specimens (males SL 1.2 and 1.4 mm, non-ovigerous female SL 0.9 mm,

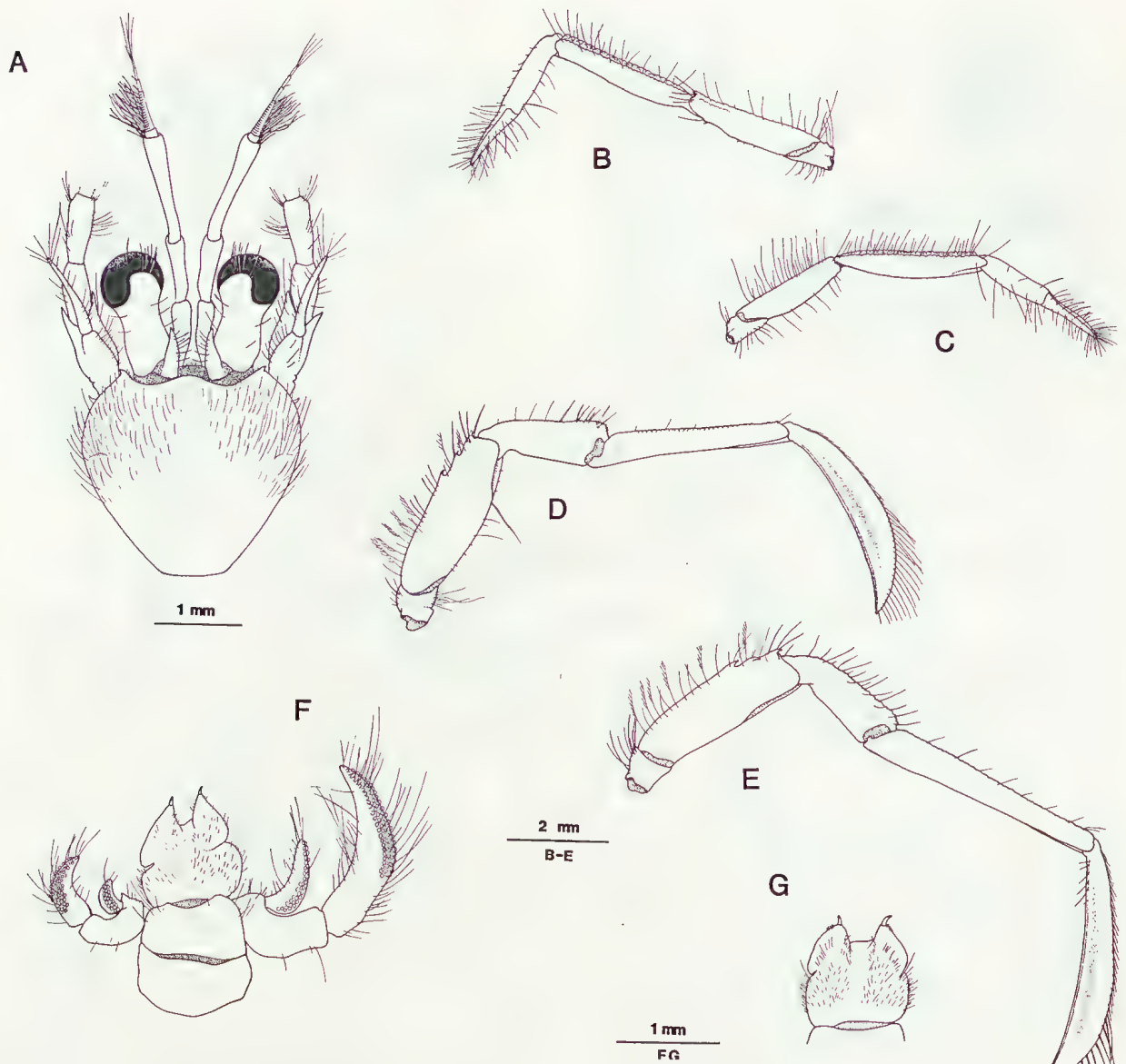


Fig.10. *Catapagurus* sp. [♀, Arafura Stn 3]. A, shield and anterior appendages; B, right cheliped (mesial view); C, left cheliped (mesial view); D, left P 2 (mesial view); E, left P 3 (mesial view); F, telson and uropods; G, telson of *Catapagurus ensifer* Henderson. [Syntype ♀, Gulf of Martaban, Burma, BMNH 1888.34].

ovigerous females SL 1.2 and 1.4 mm) to genus only. They show similarities with *Anapagurus bonnieri* Nobili from the Gulf of Iran and the Red Sea (Lewinsohn, 1969: 87, fig. 15) and with *A. japonicus* Ortmann from Japan (Miyake, 1978: 139, fig. 55).

***Catapagurus* A. Milne Edwards**

***Catapagurus ensifer* Henderson**

Catapagurus ensifer Henderson, 1893: 424, pl. 38 figs 16-19.—Alcock, 1905b: 115, pl. 15 fig. 3.—Lewinsohn, 1969: 79.

Material examined. BANDA Stn 20, 2♂, 1 unsexed (NIOJ).

Colour in life. Shield pink. Antennular peduncles white or pink with red bands. Antennal peduncles banded red; flagellum uniform red or pink. Ocular peduncles uniform red, cornea golden. Chelipeds white or salmon with narrow red longitudinal stripes on carpus and chela. Second and third pereopods white, proximal segments with red bands and narrow red longitudinal stripes, dactyl with single longitudinal row of red chromatophores.

Remarks. These crabs were observed leaping about

on a fairly fine sand substrate in 8–15 m. Of several collected, there remain only three specimens (one SL 1.2 and two SL 1.4 mm) with their pereopods detached and abdomens missing. Several species that were originally placed in *Catapagurus* have subsequently been assigned to other genera. Currently it contains about ten species from the Indo-West Pacific, some of them not yet described (Forest & de Saint Laurent, 1968: 151; de Saint Laurent, 1970: 1456). The lack of an up-to-date revision of the genus, and the poor condition of our specimens, make identification difficult, but we tentatively assign them to *Catapagurus ensifer*. They agree closely with Henderson's and Alcock's descriptions, and with the comments of Lewinsohn.

Distribution. Reported only from the Indian Ocean: Red Sea, Providence Island, Cargados Carajos, Maldive Islands, Sri Lanka and Burma. The known range is now extended eastward to Banda in Indonesia.

Catapagurus sp.

Fig. 10A–F

Material examined. ARAFURA Stn 3, 1♀ ov (AM P37730).

Colour in life. Corneas gray; distal portion of pereopods 2 and 3 transparent; rest of body mottled with red and white chromatophores.

Remarks. Trawled in 49 m. This very rapidly moving crab was observed to leap backward much like a lobster. In its shell it harboured a polychaete worm, which has been identified as a juvenile *Eunice* sp. (family Eunicidae).

Catapagurus sp. was one of four "leaper" crabs encountered during the *Alpha Helix* Expedition. *Diogenes avarus* Heller, *Anapagurus* sp., and *Catapagurus ensifer* Henderson were all found on sandy bottoms; we have no information on the substrate at the Torres Strait locality where the unidentified *Catapagurus* was collected.

Our specimen agrees with two Indo-West Pacific species, *Catapagurus ensifer* Henderson and *C. granulatus* Edmondson, in having the dactyl of pereopods 2 and 3 broad and shaped like a sabre blade. It can easily be distinguished from those species by the shape of the telson. In both *C. ensifer* (this paper, Fig. 10G) and *C. granulatus* (Edmondson, 1951: fig. 8f) the posterior lobes of the telson are shorter and more wideset, and consequently separated by a shallower and broader notch, than in the individual from Torres Strait.

The *Catapagurus* from Arafura Station 3 probably belongs to an undescribed species. However, because of the pronounced sexual dimorphism that exists in members of the genus, it seems inadvisable to furnish it with a name and description on the basis of a single specimen.

Micropagurus McLaughlin

Micropagurus vexatus n.sp.

Figs 11, 12

Material examined. HOLOTYPE: SAPARUA Stn 1, ♂ SL 1.7 mm (NIOJ A.003). PARATYPES: BANDA Stn 9, 1♂ SL 1.6 mm (AHF 755), 1♀ ov SL 1.4 mm (NIOJ A.002); SERAM Stn 2, 1♀ SL 2.5 mm (NIOJ A.013).

Description. Shield approximately as broad as long; anterior margin between rostrum and lateral projections weakly concave; posterior margin rounded or roundly truncate; dorsal surface with tufts of moderately long setae. Rostrum slightly produced, broadly rounded. Lateral projections broadly rounded, unarmed.

Ocular peduncles about $\frac{1}{10}$ length of shield, slender, slightly to strongly inflated basally, constricted at base of cornea; with tufts of short setae dorsomesially. Ocular acicles subquadrate, with 5–7 spines on margin and fringe of long setae just proximal to spine row; widely separated basally.

Antennular peduncles falling short of or barely reaching to base of cornea. Ultimate and penultimate segments unarmed; basal segment with strong spine at ventrolateral distal angle.

Antennal peduncles not reaching to base of cornea. Fifth and fourth segments unarmed and with tufts of setae. Third segment unarmed or with small spine at ventromesial distal angle. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine; dorsomesial angle with small spine. First segment with small, simple or bifid spine on lateral margin distally. Acicle moderately short, terminating in small spine; mesial margin unarmed or with 1 or 2 small spines, lateral margin unarmed or with spine proximally. Flagellum with few long and short setae distally on each article.

Third maxillipeds with small tooth on basis; ischium with moderately developed crista dentata and with accessory tooth; merus and carpus each with strong dorsodistal spine.

Chelipeds moderately short in comparison to their width. Right cheliped with dactyl usually slightly shorter than palm; cutting edge with 2 calcareous teeth proximally and with row of very small corneous teeth distally; terminating in small corneous claw; dorsomesial margin with 2–4 spines on proximal half, with fringe of long setae; dorsal surface unarmed, with long setae. Palm about $\frac{2}{3}$ length of carpus; dorsomesial margin with row of spines and with long setae, mesial face with scattered tubercles; dorsal surface flattened, with longitudinal row of small spines proximally and with few small tubercles distally; dorsolateral margin with row of spines extending onto fixed finger for approximately half its length, with fringe of long setae; fixed finger with row of small calcareous teeth on cutting edge and long setae on dorsal surface; terminating in corneous claw. Carpus approximately as long as merus;

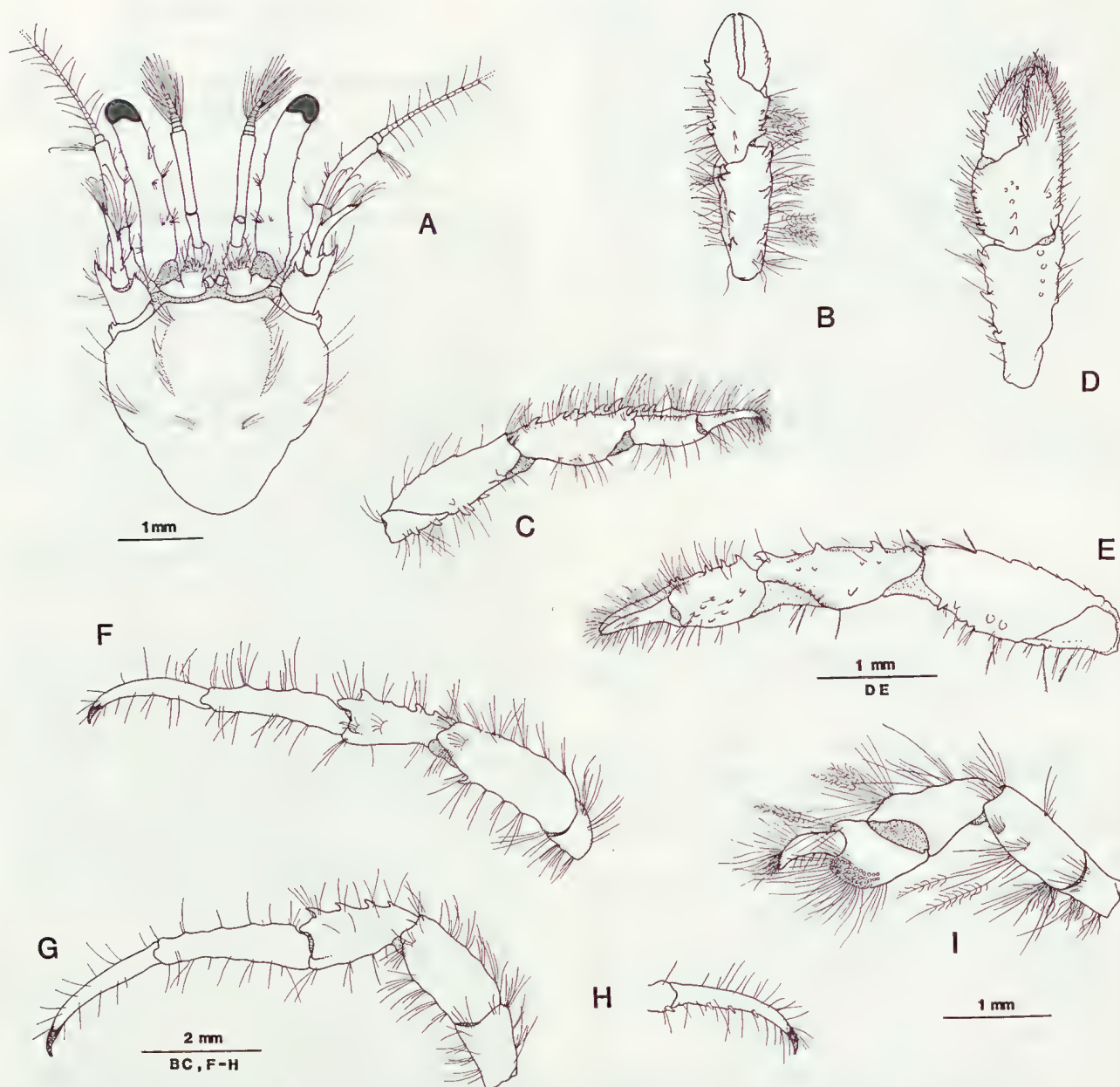


Fig.11. *Micropagurus vexatus* n.sp. [A–C, F–I, ♀, Seram Stn 2; D, E, holotype ♂, Saparua Stn 1]. A, shield and anterior appendages; B, left chela and carpus (dorsal view); C, left cheliped (mesial view); D, right chela and carpus (dorsal view); E, right cheliped (mesial view); F, left P 2 (lateral view); G, left P 3 (lateral view); H, dactyl of left P 3 (mesial view); I, left P 4 (lateral view).

dorsomesial margin with 3 strong, widely spaced spines; dorsolateral margin obscurely tuberculate; mesial and lateral faces with scattered tubercles. Merus with row of protuberances on dorsal margin; mesial face with few strong tubercles near ventral margin, ventromesial margin with strong spine on distal half; lateral face tuberculate ventrally.

Left cheliped (missing in holotype) with dactyl approximately $1\frac{1}{2}$ times as long as palm; cutting edge with row of small corneous teeth; terminating in small corneous claw; dorsomesial margin with row of

3 spines medially and with fringe of long setae; dorsal surface unarmed, with long setae. Palm slightly less than $\frac{1}{2}$ length of carpus; dorsomesial margin with 3 or 4 spines and with long setae; dorsal surface flattened, with 2 spines in longitudinal row proximally; dorsolateral margin with row of spines extending onto fixed finger for less than half its length, and with fringe of long setae; fixed finger with row of small corneous teeth on cutting edge and long setae on dorsal surface; terminating in corneous claw. Carpus approximately as long as merus;

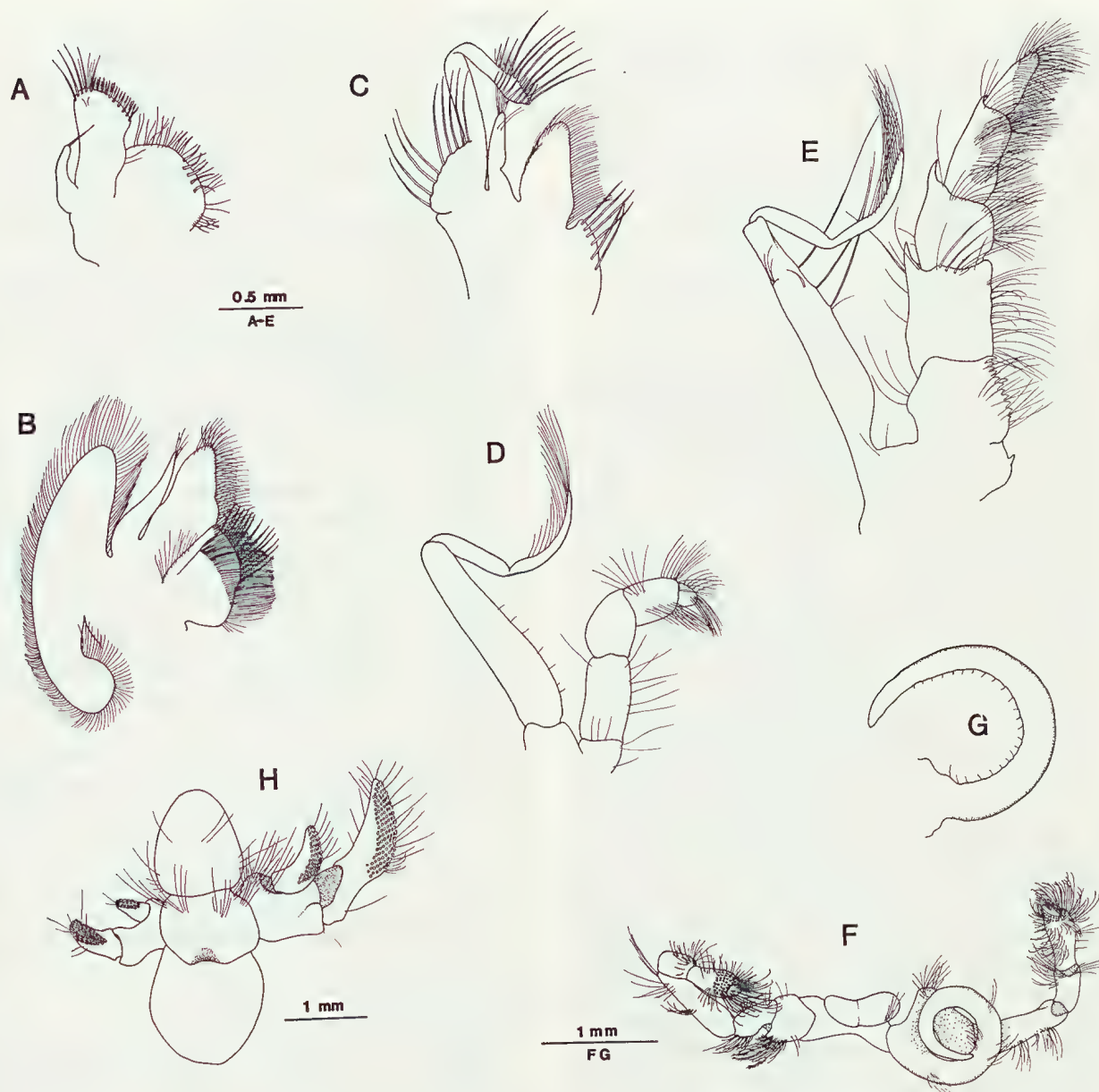


Fig.12. *Micropagurus vexatus* n.sp. [A-E, H, ♀, Seram Stn 2; F, holotype ♂, Saparua Stn 1; G, ♂, Banda Stn 9]. A, maxillule, B, maxilla, C, mxp 1, D, mxp 2, E, mxp 3 (all left, internal view); F, male coxae of P 5 and sexual tube, in situ; G, male sexual tube; H, telson, uropods, and 5th abdominal somite.

dorsomesial margin with 4 strong spines, most distal one very large and terminally bifid; dorsolateral margin with 4 spines; both margins with fringe of setae. Merus with row of protuberances on dorsal margin, mesial face with 2 spines near ventral margin, ventromesial margin with 2 narrow, closely set spines proximally; lateral face tuberculate ventrally, ventrolateral margin with median spine. Ischium with 3 spines on ventral margin.

Second pereopods with dactyl long and slender, shorter than propodus; in lateral view slightly curved ventrally, in dorsal view almost straight; terminating in strong corneous claw; ventral margin with row of 3-5 widely spaced, corneous spines. Propodus about

1½ times length of carpus; ventral margin with corneous spine distally; lateral and mesial faces with scattered tubercles. Carpus approximately ⅔ length of merus; dorsal margin with 3 or 4 spines; lateral face with scattered tubercles. Merus laterally compressed; dorsal and ventral margins with low protuberances, ventral margin usually with strong spine on distal half; lateral face with scattered tubercles. Dorsal and ventral margins of all segments with tufts of setae.

Third pereopods with dactyl long and slender, approximately equalling length of propodus; in lateral view slightly curved ventrally, in dorsal view almost straight; terminating in strong corneous claw;

ventral margin with row of corneous spines. Propodus about $1\frac{1}{2}$ times length of carpus; ventral margin with corneous spine distally. Carpus about as long as merus, or slightly shorter; dorsal margin with 4 spines (all but anterior one broken off in holotype). Merus laterally compressed; dorsal and ventral margins with low protuberances. Dorsal and ventral margins of all segments with tufts of setae.

Fourth pereopods with propodal rasp composed of several rows of scales.

Sternite of pereopod 3 with anterior lobe broad, subrectangular. Sternite of pereopod 5 forming 2 distinct lobes, left larger than right.

Males with coxae of pereopod 5 unequal, left larger than right, with well developed, moderately elongate sexual tube directed outward then doubling back on itself, or forming complete loop; right coxa without gonopore. Uropods asymmetrical, left much larger than right. Telson longer than broad, without transverse suture; terminal margin entire, narrow and rounded, unarmed.

Colour in life. (Saparua and Seram) Shield mottled gray and cream or green and white. Ocular peduncles transparent with black mottlings, or mottled green and white; cornea salmon pink or off white. Antennules transparent but for black stripe or row of black dots dorsally. Antennal peduncles with green mottlings; flagellum transparent. Merus of chelipeds with brownish mottling on a white background; carpus and chela dirty white. Second and third pereopods basically transparent with mottled brown and cream; propodus and dactyl each with narrow brown longitudinal stripe on lateral face.

(Banda) Ocular peduncles uniform olive drab. Antennules white except for purple stripe dorsally. Antennal peduncles mottled red and white; flagellum transparent. Right cheliped purplish pink; left with proximal segments mottled olive drab and transparent, palm pink. Ischium and merus of pereopods 2 and 3 purplish pink; carpus with fine red mottlings on white/transparent background; propodus and dactyl with narrow dark longitudinal stripe on lateral face.

Remarks. The holotype was collected inshore on rocks covered with coral, the paratype from Seram in about 1 m in a sandy area near coral and eel grass, and the two specimens from Banda between 0–12 m on a bottom of rock, coral and coral rubble.

The specimens from Seram and Saparua each had a bright orange parasite attached to the abdomen. This was identified as the egg sac of an epicaridean isopod, family Cryptoniscidae. In the crab from Seram Station 2, with a total carapace length of approximately 4.8 mm, the egg sac was 6.5 mm long.

Recently McLaughlin (1986: 793–794) described a new genus and species of hermit crab, *Micropagurus devaneyi*, from the Hawaiian Islands. We describe our species as new because it differs from *M. devaneyi* in several details, notably in the shape of the telson. In the Hawaiian species this is broader than

long, widest about midway along the lateral margins, and with proximal and terminal margins approximately equal (McLaughlin, 1986: fig. 3i); in *M. vexatus* it is longer than broad, widest near the proximal end and narrow terminally. Unlike *M. devaneyi*, the new species has a fringe of long setae on the ocular acicles, these arising just proximal to the marginal spines. To judge from the small sample on which each species was based, the antennular and ocular peduncles are relatively more slender in *M. vexatus* than in *M. devaneyi*, and the ocular peduncles longer in comparison to the shield. There are also minor differences in the armature of the pereopods and in the number of rows of scales on the propodus of pereopod 4.

In her description of *Micropagurus devaneyi*, McLaughlin (1986: 797) drew attention to the presence of multispinose ocular acicles in *Anapagurus australiensis* Henderson and *A. polynesiensis* Nobili, and remarked that in this character and in general morphology those species resemble her new genus. She pointed out that de Saint Laurent (1968) had reported the absence of the right gonopore (also a characteristic of *Micropagurus*) in males of *A. polynesiensis*. For these reasons, McLaughlin suggested that *A. australiensis* and *A. polynesiensis* should possibly be assigned to *Micropagurus*.

Henderson (1888: 74, pl. 7 figs 8, 8a,b) described *Anapagurus australiensis* from Port Jackson, N.S.W. Examination of the two syntypes (♂ SL 1.9 mm, ♀ SL 2.1 mm, BMNH 1888.33) confirmed that this taxon is congeneric with the genus *Micropagurus*. The telson is of the same form and approximately the same shape as that of *M. vexatus*, but *M. australiensis* differs from our new species in having the antennular peduncles longer than the ocular peduncles, only four spines on the margin of the ocular acicles, and the carpus of pereopods 2 and 3 unarmed.

Nobili (1906: 260) published a diagnosis of *Anapagurus polynesiensis* from Rikitea in French Polynesia. The following year he presented a longer description with illustrations (Nobili, 1907: 372, pl. 1 figs 10, 10a–c) and noted its relationship to *A. australiensis*. Michèle de Saint Laurent (in communication to J. Haig) repeated her statement (1968: 549) that the male of Nobili's species lacks a gonopore on the right side, and added that the posterior margin of the telson is entire and rounded. This species is hereby transferred to *Micropagurus*. Sketches of the shield, anterior appendages, and chelipeds of *M. polynesiensis*, provided by M. de Saint Laurent, show that it differs from our new species in the greater number of spines on the chela and carpus of the chelipeds, and in lacking a fringe of setae on the ocular acicles.

Etymology. From Latin *vexatus* meaning molested or annoyed, in reference to the parasites, considerably larger than their hosts, that were found on two of the type specimens.

Nematopagurus A. Milne Edwards & Bouvier*Nematopagurus gardineri* Alcock

Nematopagurus gardineri Alcock, 1905a: 834, pl. 68 fig. 3; 1905b: 110, pl. 12 fig. 2.—Miyake, 1978: 129, 130.

Material examined. ARAFURA Stn 12, 1♂, 1♀ ov (AM P37750); Stn 13, 1♂ (AHF).

Colour in life. Carapace with scattered red and white chromatophores on semi-transparent background. Ocular peduncles transparent dorsally, red ventrally; cornea silvery. Antennules transparent proximally, light reddish brown distally. Antennae reddish brown. Merus and carpus of chelipeds with large red spots on semi-transparent background. Carpus, propodus and dactyl of pereopods 2 and 3 with reddish brown longitudinal stripes on semi-transparent background.

Remarks. These crabs were trawled in 58–64 m. One specimen from Station 12 had many anemones on its shell.

Our specimens agree with the original description except for the shape of the ocular peduncles. Alcock describes these as "...not much expanded", but in the *Alpha Helix* material they are markedly expanded at the cornea. Miyake (1978), in what is apparently the first record of this species since the two descriptions of the holotype, did not mention the form of the ocular peduncles.

Distribution. Reported only from the Maldiv Islands and from Sagami Bay, Japan; now Arafura Sea.

Pagurus Fabricius*Pagurus hedleyi* (Grant & McCulloch)

Fig. 13

Eupagurus kirkii Miers, 1884: 267, pl. 28 fig. C. (Name preoccupied by *E. kirkii* Filhol, 1883).

Eupagurus hedleyi Grant & McCulloch, 1906: 37. (New name for *E. kirkii* Miers).

Pagurus hedleyi.—Gordan, 1956: 330.—Sankolli, 1962: 141.

Material examined. ARAFURA Stn 1, 1♂ (AM P37707).

Colour in life. Ocular peduncles white with broad, subproximal orange band; cornea black with white speckles. Antennules bluish; penultimate segment of peduncle with broad orange band distally. Chelipeds turquoise with brown spots; setae white. Pereopods 2 and 3 turquoise with brown bands.

After a few years of preservation in alcohol, turquoise ground colour faded to white. Shield with brown spots and blotches anteriorly and laterally. Antennal peduncles and acicles spotted with brown; flagellum banded brown and white. Ocular acicles mostly brown. Bands on pereopods 2 and 3 broken up into spots similar to those of chelipeds.

Remarks. Trawled in 27 m on an unspecified substrate.

Because of discrepancies between our specimen and the original description, one of us (J. Haig) examined the holotype, a male with SL 4.1 mm (BMNH 1882.7). It shows the following characters which are contrary to Miers' description and illustration: (1) the anterior margin of the carapace shield is produced medially into a short, broad rostrum. There is a small but distinct lateral projection on either side, and the anterior margin between the rostrum and these projections is slightly concave; (2) the ocular peduncles are about $\frac{4}{5}$ the length of the shield; (3) the larger (right) cheliped has a well-developed ventromesial lobe or crest on both merus and carpus. These lobes are not mentioned in the description and they are only slightly indicated in dorsal aspect in the accompanying illustration, and (4) the second and third pereopods (only the left ones are present) have a small dorsodistal spine on the carpus and a row of movable spinules on the ventral margin of the propodus and dactyl.

The *Alpha Helix* specimen is smaller (SL 3.5 mm) than the holotype, but differs from it in only a few details. The relative proportions of the ocular, antennular and antennal peduncles are close to those of the type. Our specimen has rather long setae on the proximal part of the antennal flagella; these are not present in the holotype. The armature of the dorsal surface of the chelipeds is hidden by a dense covering of fine setae, and the setation on the second and third pereopods is considerably heavier than in the holotype. The telson of our specimen is missing.

Sankolli (1962: 141–2) pointed out that his *Pagurus kulkarnii* n.sp. is closely allied to *P. hedleyi*. He distinguished the two forms by the presence in *P. kulkarnii* of a ventromesial crest on the merus of the right cheliped, and the absence of such a crest in *P. hedleyi*. However, as noted above, *P. hedleyi* does possess a meral (and also a carpal) crest, and the two species are also similar in the form of the anterior margin of the shield, ocular and antennal peduncles and telson, and in having a single row of scales in the propodal rasp of the fourth pereopods. The description of *P. kulkarnii*, and a few specimens from India and Pakistan in the collections of the Allan Hancock Foundation, conform with the two available specimens of *P. hedleyi* except in a few minor details that could be accounted for by individual variation. Comparison of a good series of each species may be necessary before they can be definitely separated on morphological grounds.

At present, the two species are best distinguished by their live colouration. For *Pagurus kulkarnii*, this is described by Sankolli (1962: 142) as "...light brown with longitudinal stripes of chocolate brown colour on major portions of the cheliped and on the second and third pereopods." Tirmizi & Siddiqui (1982: 92) describe the pereopods of *P. kulkarnii* as being orange distally and green proximally, the green parts marked with chocolate brown longitudinal stripes. This is in sharp contrast with the turquoise

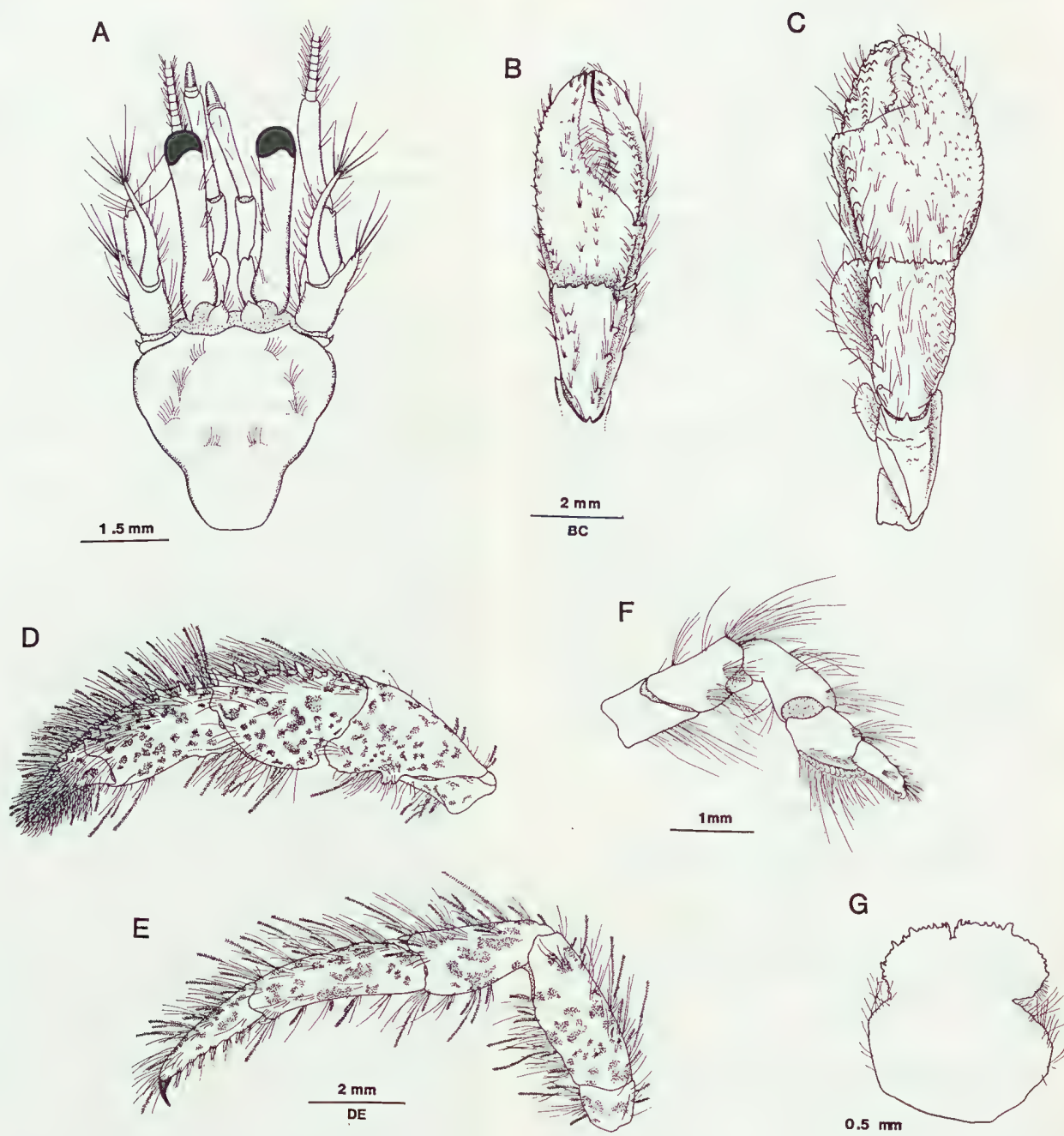


Fig.13. *Pagurus hedleyi* Grant & McCulloch. [A,D-F, ♂, Arafura Stn 1; B,C,G, ♂, holotype of *Eupagurus kirkii* Miers, Arafura Sea, BMNH 1882.7]. A, shield and anterior appendages; B, left chela and carpus (dorsal view); C, right cheliped (dorsal view); D, right cheliped (mesial view); E, left P 2 (lateral view); F, right P 4 (lateral view); G, telson.

blue ground colour, and the brown spots and bands on the pereopods, that were observed in our specimen of *P. hedleyi*.

Distribution. Arafura Sea, Torres Strait and coast of Queensland.

Pagurus hirtimanus Miers

Pagurus hirtimanus White, 1847: 60 (*nomen nudum*).—Miers, 1880: 375, 376.—Lewinsohn, 1969: 62.
Eupagurus japonicus?.—Miers, 1880: 375, pl. 14 figs 6, 7. [not *Pagurus japonicus* (Stimpson)].

Eupagurus hirtimanus.—De Man, 1888: 426.

Eupagurus sp. a.—De Man, 1902: 730.

[?] *Eupagurus* sp. b.—De Man, 1902: 730.

Eupagurus janitor Alcock, 1905a: 832, pl. 68 figs 2, 4; 1905b: 125, 132, pl. 11 fig. 6.

Pagurus janitor.—Gordan, 1956: 331.

Material examined. BANDA Stn 1, 1♂ (NIOJ). SERAM Stn 2, 1♀ (NIOJ).

Colour in life. Carapace mottled tan and white. Proximal part of ocular peduncles white, distal part blue; these areas separated by black or blue-green median band; cornea black. Antennular peduncles blue, flagellum orange or tan. Antennal peduncles pale blue, flagellum yellow orange. Chelipeds mottled brown and white. Proximal segments of pereopods 2 and 3 brown with large white areas; propodus white with median brown band; dactyl white.

Remarks. The specimen from Banda occurred on coral or black lava sand at 0–4 m in a relatively protected area. At Seram the species was encountered in 15 m or less.

Distribution. Red Sea to Fiji Islands; north to Ryukyu Islands and south to Queensland, Australia.

Pagurus moluccensis n.sp.

Figs 14, 15A,B,D

Material examined. HOLOTYPE: BANDA Stn 5b, ♂ SL 2.1 mm (NIOJ A.009).

Description. Shield approximately as long as broad; anterolateral margins sloping; anterior margin between rostrum and lateral projections slightly concave; posterior margin roundly truncate; dorsal surface generally smooth except for grooves defining lateral areas; anterolateral angles slightly produced, bluntly rounded. Rostrum obtusely triangular, slightly exceeding lateral projections. Lateral projections broadly rounded, unarmed.

Ocular peduncles about $\frac{2}{3}$ length of shield; slightly inflated basally; dorsal and mesial faces with scattered short setae. Ocular acicles large, triangular, terminating in strong, apparently subterminal spine; broadly separated basally. Ophthalmic somite with prominent interocular structure, this subrectangular basally and with 2 elongate processes separated by deep, narrow median cleft.

Antennular peduncles equalling length of ocular peduncles. Ultimate and penultimate segments unarmed; basal segment with small spine at ventromesial distal angle.

Antennal peduncles exceeding ocular peduncles by about half length of ultimate segment; with supernumerary segmentation. Fifth and fourth segments unarmed. Third segment with tuft of long setae near distal end of ventral margin. Second segment with dorsolateral distal angle produced, terminating in simple spine; dorsomesial distal angle subrectangular, unarmed; lateral and mesial margins

with long setae. First segment with strong spine on lateral face distally; ventromesial margin inflated; ventrodistal margin with small spine. Acicle slightly exceeding distal margin of fourth peduncular segment; arcuate and terminating in simple acute spine and tuft of long setae; mesial margin with moderately long setae. Flagellum moderately long; each article with very short setae distally.

Third maxilliped with basis-ischium fusion apparently incomplete (this not evident from illustration); basis with minute spine (not shown in illustration); ischium with crista dentata moderately well developed, 2 accessory teeth; other segments unarmed. Sternite of maxilliped 3 apparently unarmed.

Dactyl of right cheliped approximately as long as palm, slightly deflexed, mesial margin strongly curved; cutting edge with row of calcareous teeth, tip calcareous; slightly overlapped and over-reached by fixed finger; dorsomesial margin delimited, with row of closely set granules; dorsal surface convex, granular; ventral surface nearly smooth. Fixed finger slightly deflexed, lateral margin strongly curved; cutting edge with row of calcareous teeth, tip calcareous; dorsal and mesial surfaces granular; ventral surface nearly smooth. Palm approximately length of carpus, dorsoventrally flattened; dorsal surface convex, covered with closely set granules; dorsomesial margin straight, delimited, with granules slightly more prominent distally; dorsolateral margin delimited, row of granules forming inconspicuous crest, latter extending to tip of fixed finger; lateral, mesial and ventral surfaces nearly smooth. Carpus approximately as long as merus, slightly inflated dorsoventrally; dorsal surface flattened, obscurely granular, distal margin unarmed; dorsomesial margin delimited, distal half with few small spines; mesial surface flattened, nearly smooth; dorsolateral margin not delimited; lateral and ventral surfaces nearly smooth. Merus subtriangular; dorsal surface nearly smooth, distal margin with 2 minute spines; mesial and lateral faces nearly smooth, distal margins with few spines or pointed tubercles; ventral surface with few flattened tubercles.

Left cheliped surpassing base of dactyl of right chela. Dactyl slightly over twice length of palm; cutting edge with row of small corneous teeth, with few small calcareous teeth proximally; terminating in small corneous claw; dorsomesial margin delimited by row of granules; dorsal and mesial surfaces granular; ventral surface nearly smooth. Fixed finger with lateral margin strongly curved distally; cutting edge with row of calcareous teeth; terminating in small corneous claw; dorsal surface granular; ventral surface nearly smooth. Palm approximately half as long as carpus, dorsoventrally flattened; dorsal surface flattened, covered with closely set granules; dorsomesial margin straight, delimited; dorsolateral margin delimited, with inconspicuous crest

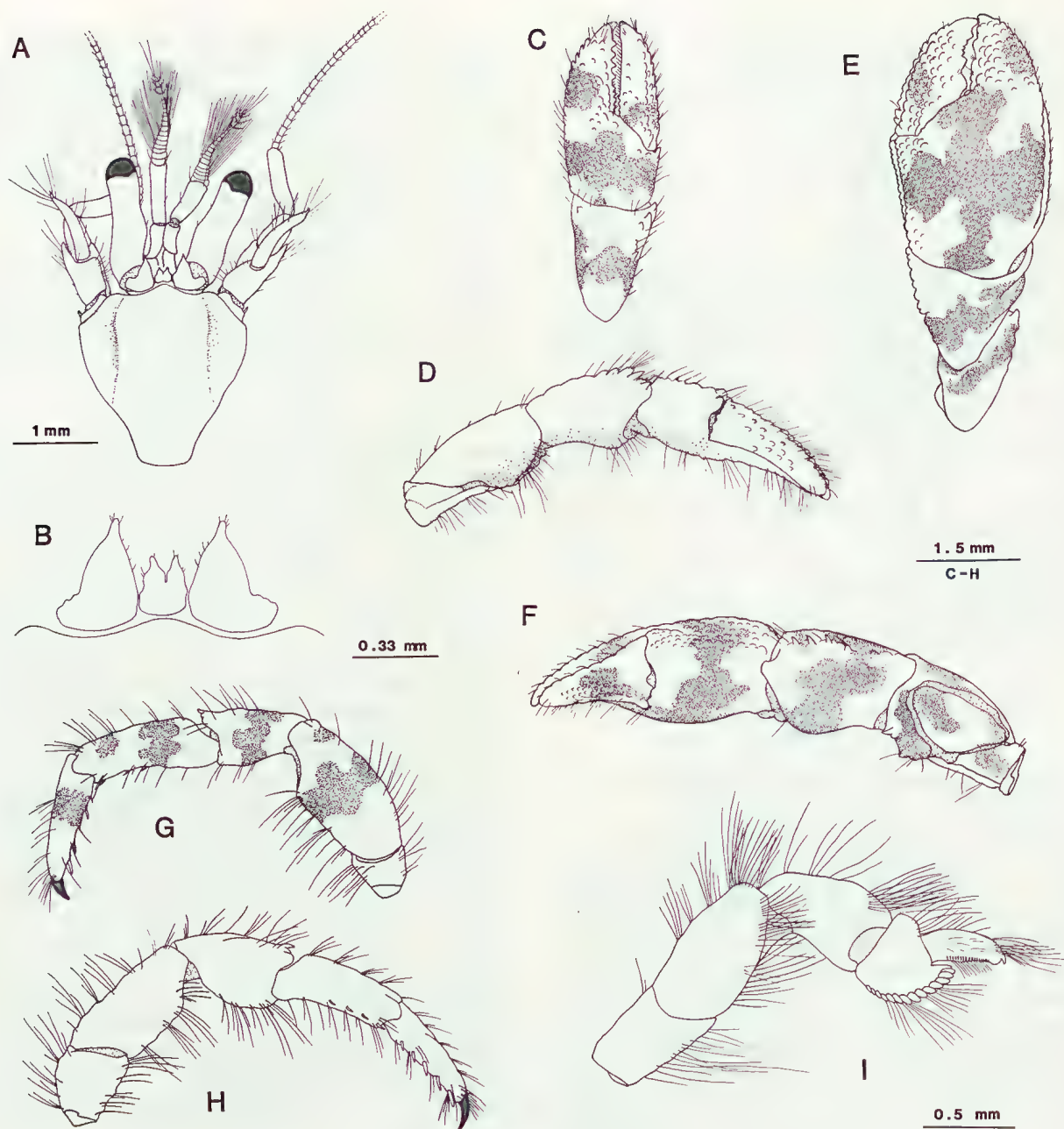


Fig.14. *Pagurus moluccensis* n.sp. [Holotype ♂, Banda Stn 5b]. A, shield and anterior appendages; B, ocular acicles and interocular process; C, left chela and carpus (dorsal view); D, left cheliped (mesial view); E, right cheliped (dorsal view); F, right cheliped (mesial view); G, left P 2 (lateral view); H, left P 3 (mesial view); I, right P 4 (lateral view).

extending nearly to tip of fixed finger; lateral surface nearly smooth except for granules on distal part of fixed finger; mesial and ventral surfaces nearly smooth. Carpus approximately as long as merus; dorsal surface flattened, obscurely granulate, distal margin unarmed; dorsomesial margin delimited, distal half with few spines; dorsolateral margin not delimited; lateral, mesial and ventral surfaces nearly smooth. Merus subtriangular; dorsal, mesial and lateral surfaces nearly smooth; ventrolateral and

ventromesial margins each with few spiniform granules.

Second pereopods moderately short and stout. Dactyl shorter than propodus; straight in lateral view and slightly twisted in dorsal view; terminating in strong corneous claw; dorsal, lateral and mesial surfaces smooth; ventral margin with row of strong corneous spines increasing in size distally. Propodus exceeding length of carpus; dorsal margin obscurely granulate, lateral and mesial surfaces smooth,

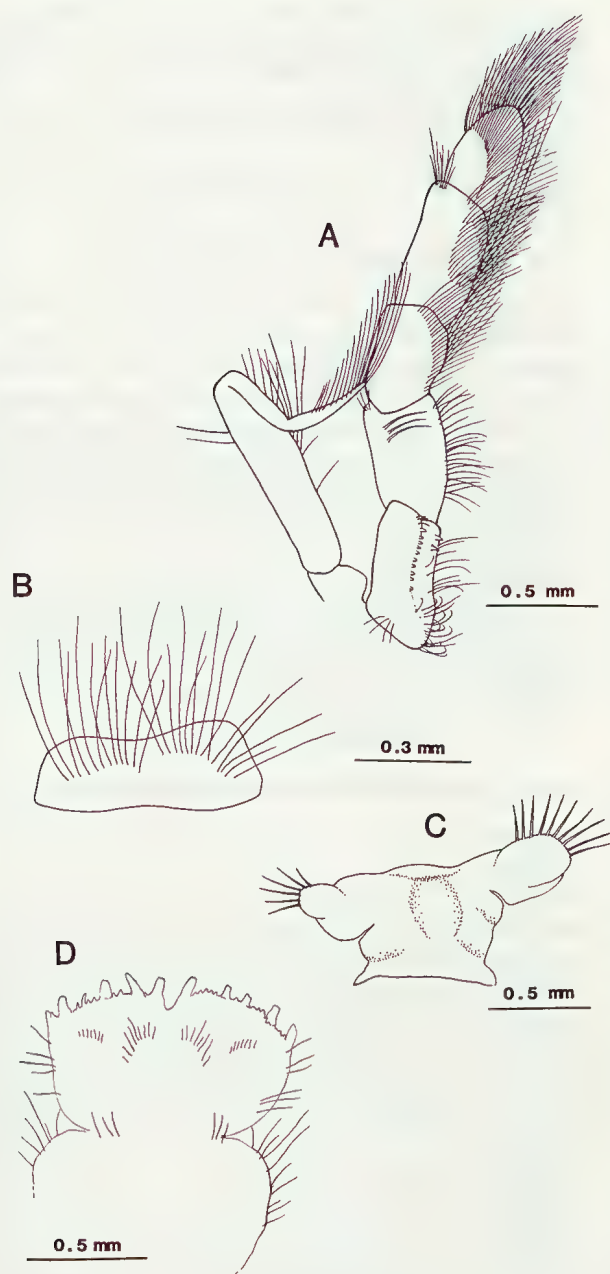


Fig.15. *Pagurus moluccensis* n.sp. [Holotype ♂, Banda Stn 5b]. A, mxp 3 (left, internal view); B, sternite of P 3; D, telson; C, sternite of P 5 of *Pagurus* sp. [♂, Philippine Islands, USNM].

ventral surface with row of small corneous spines increasing in size distally. Carpus about $\frac{3}{4}$ length of merus; dorsal surface obscurely granulate, with small spine distally; lateral, mesial and ventral surfaces smooth. Merus laterally compressed; dorsal and ventral margins obscurely granulate, lateral and mesial surfaces smooth.

Third pereopods approximately equalling length of second; similar to second in armature and proportional measurements.

Fourth pereopods apparently with preungual process at base of claw on lateral face of dactyl. Propodal rasp with single row of scales.

Sternite of third pereopods with anterior lobe subrectangular, considerably broader than long; with long setae. Sternite of fifth pereopods with anterolateral angles produced (right more strongly so than left), subovate, clearly delineated.

Unpaired pleopods 3–5 present in male, with exopod well developed and endopod rudimentary. Female pleopods unknown.

Telson with posterior lobes subquadrate, left slightly larger than right; separated by moderately broad, deep median cleft; terminal margins nearly straight, each with 5 prominent spines (tips broken off in holotype) and with numerous, much smaller spines.

Colour in life. Shield with black markings on white background. Ocular peduncles with broad, subproximal dark band. Antennular peduncles white, penultimate segment with broad, submedian dark band. Antennal peduncles with alternating black and white bands. Chelipeds with complex black pattern on white background (Fig. 14C,E,F). Pereopods 2 and 3 with black, irregular-edged bands on white background (Fig. 14G).

Remarks. The specimen occurred in a protected area with a fairly strong current, in 1–5 m on coral sand and rock.

This species is only provisionally assigned to *Pagurus*. It differs from all previously known members of that genus by the possession of a prominent, two-spined interocular process, a structure that has been reported only in two species of *Anapagurus* (see Dehancé & Forest, 1962). The form of the sternite of the fifth pereopods is also unusual for the genus. In *Pagurus* species of the “provenzanoï” group the sternite of pereopod 5 has strongly produced anterolateral angles (McLaughlin, 1975: 373, fig. 7), but in those species the general shape of the sternite is different from that of *P. moluccensis*.

A small hermit crab from the Philippine Islands (♂ SL 2.4 mm, USNM) was sent for comparison by Michèle de Saint Laurent. Although it does not appear to be conspecific with *P. moluccensis*, it agrees with the new species in having a bispinate interocular structure and produced anterolateral angles on the sternite of pereopod 5. Since the sternite of the holotype was damaged during study, the corresponding, almost identically shaped part was illustrated from the Philippine specimen.

The occurrence of the distinctively shaped interocular structure and sternite of pereopod 5 in our new species suggests that it may be generically distinct from *Pagurus*. We have preferred not to dissect the unique specimen to look for other characters which might support this hypothesis.

Etymology. From the Moluccas, the old name of the island group now known as Maluku.

Pagurus pergranulatus (Henderson)

Eupagurus pergranulatus Henderson, 1896: 520.—Alcock & Anderson, 1897: pl. 31 fig. 1.—Alcock, 1905b: 125, pl. 11 fig. 1.

Pagurus pergranulatus.—Gordan, 1956: 333.

Material examined. SERAM Stn 2, 2♂, 1♀ ov (NIOJ).

Colour in life. Carapace mottled purple and white. Ocular peduncles basically white; narrow tan line at base of stalk, tan band next to cornea, and broad orange band medially; cornea mottled silver. Antennular peduncles bright orange, with narrow white band at distal end of penultimate segment and at both ends of distal segment; flagellum bright orange. Antennal peduncles white, with mottled purple basally; flagellum with alternating bands of purple and transparent. Major cheliped mottled purple and white. Merus, carpus and propodus of minor cheliped with purple lines on white background; chela with 2 irregular purple blotches on lateral face. Proximal segments (ischium through propodus) of pereopods 2 and 3 with purple lines like those of minor cheliped; dactyl with single median line and 2 broad bands (1 subdistal, 1 proximal).

Narrow lines of colour on minor cheliped and second and third pereopods usually not reaching ends of segments; somewhat irregular in form, periodically broadening and becoming thinner again on each segment.

Remarks. The specimens were collected in 15 m or less. One was parasitised by a rhizocephalan.

Our material (♂ SL 3.7 and 5.9 mm, ♀ SL 3.8 mm) agrees well with two specimens in the collections of the Indian Museum: the 3.9 mm female holotype from *Investigator* Station 175, off Sri Lanka (IM 1121/10), and a 4.4 mm male from the Andaman Islands (IM 9023/6) which was recorded by Alcock (1905b: 126). We have also seen a 7.5 mm female specimen in the Australian Museum (AM E4488) from 40 km south-east of Double Island Point, Queensland.

While the *Alpha Helix* material of *Pagurus pergranulatus* was collected in 15 m or less, specimens reported by Henderson & Alcock came from depths of about 36.5–58.5 m and the Australian one from 100 m.

Distribution. Sri Lanka; Andaman Islands; Seram; Queensland, Australia. The latter two localities are extensions of the previously known range of the species.

Pylopaguropsis Alcock*Pylopaguropsis* undescribed sp. 1

Material examined. SERAM Stn 2, 1♀ (NIOJ). SAPARUA Stn 1, 1♂, 2♀ (1 ov) (NIOJ, AHF). SAPARUA Stn 3, 1♂, 1♀ ov (NIOJ, AM P37795).

Colour in life. Chela of major cheliped white; mesial face of merus and carpus with longitudinal

(presumably purple and orange) stripes. Minor chela and second and third pereopods with longitudinal purple and orange stripes, these extending to both ends of all segments.

In preservative, longitudinal stripes red on white background.

Remarks. Found in 0–8 m, probably on coral.

Pylopaguropsis undescribed sp. 2

Material examined. SERAM Stn 2, 1♂ (NIOJ). SAPARUA Stn 3, 1♀ (NIOJ).

Colour in life. Presumably similar to that of *Pylopaguropsis* sp. 1; both species occurred together at 2 stations, and in the field were not recognised as being distinct. Preserved specimens still show traces of longitudinal red stripes on pereopods 2 and 3, but no pattern on the mesial face of the merus and carpus of the right cheliped.

Remarks. Taken in 0–5 m, probably on coral.

These two species of *Pylopaguropsis* will be described in a forthcoming revision of the genus (McLaughlin & Haig, in press).

Spiropagurus Stimpson*Spiropagurus fimbriatus* Lewinsohn

Spiropagurus fimbriatus Lewinsohn, 1982b: 213, fig. 1.

Material examined. ARAFURA Stn 7, 1♂ (AHF); Stn 11, 1♂ (AHF); Stn 13, 2♂ (AM P37733). PULAU MARSEGU, off Seram, 15 May 1975, coll. A.G. Humes, 1♂, 1♀ (NIOJ).

Colour in life. Basically pink. Ocular peduncles transparent with scattered white chromatophores; cornea silver. Antennules and antennae transparent with scattered white chromatophores. Carpus of chelipeds with orange spines; chela with pale orange-brown longitudinal stripes on silvery white background.

Remarks. Trawled in 49–64 m in Arafura Sea; collected in 5 m of water at Seram.

Until recently *Spiropagurus spiriger* (De Haan) was the only known Indo-West Pacific member of the genus, as the latter was defined by de Saint Laurent-Dechancé (1966a: 158). It has been reported from a number of localities in the Indian Ocean, and eastward to Japan and the Admiralty Islands. Alcock (1905b) designated three varieties of *S. spiriger* from the Indian Ocean. Lewinsohn (1982b) described a new species, *S. fimbriatus*, from the Red Sea and compared it with Japanese specimens of *S. spiriger*. Lewinsohn commented that Alcock's varieties have certain characters which do not agree with typical *spiriger*, and suggested that some or all of them may turn out to be valid species when they become better known.

Our five male specimens of *Spiropagurus fimbriatus* are about the same size as the single female (CL 5.5 mm, CB 7.0 mm) on which

Lewinsohn's description was based, and agree very closely with it. The length of the shield varies from 75% to 79% of its breadth. The carpus of the chelipeds has five to eight spines on the dorsomesial margin and four to six on the dorsolateral margin. The merus of pereopods 2 and 3 is armed with one to four spines on the distal part of the dorsal margin. The male sexual tube looks much like that of *S. spiriger* (Alcock, 1905b: pl. 13 fig. 1a). Males have three uniramous unpaired pleopods, the most posterior one very small.

Henderson's general remarks (1888: 72) on the variations in his material of *Spiropagurus spiriger* suggest that it included more than one species or variety. An attempt was made to borrow the specimens that Henderson reported from Torres Strait and the Arafura Sea; but according to Mr Paul Clark, those specimens are not in the collections of the British Museum (Natural History) and their present whereabouts is unknown. Thus the presence of *S. spiriger* in that area still has to be confirmed.

The occurrence of *Spiropagurus fimbriatus* in shallow water at Pulau Marsegu was perhaps unusual, for its known bathymetric range in the Red Sea, Arafura Sea and Torres Strait is 49 to about 82 m.

Distribution. Red Sea; now Arafura Sea, Torres Strait, and Seram.

Discussion

Of the 52 species collected during the *Alpha Helix* Expedition, 37, or about 71%, are known to inhabit the Indian Ocean. (For two of these species the Indian Ocean records are still unpublished). Thirty-two species extend to, or nearly to, the east African coast, Red Sea or Persian Gulf, three range westward as far as India and Sri Lanka, and two occur in only the eastern part of the Indian Ocean. Fourteen of these Indian Ocean species reach the eastern end of their range in eastern Indonesia, Australia/New Guinea, or the Ryukyu Islands, eight continue eastward to the islands of western or mid-Oceania, and 15 extend across the Pacific Ocean to the Hawaiian Islands, Line Islands, and/or French Polynesia.

Most of the *Alpha Helix* hermit crabs that are not known to occur in the Indian Ocean have rather restricted distributions, although one of these species occurs as far east as Hawaii. Two are known from Australia only, and seven (including four described herein) from eastern Indonesia only. One is known from Borneo, Maluku and Guam. Four have the western end of their range in Maluku, whence they extend respectively eastward to eastern New Guinea, Queensland and Vanuatu, and northward to southern Japan.

With the exception of *Spiropagurus fimbriatus* there was no overlap between the species trawled in the Arafura Sea and those collected elsewhere during

the *Alpha Helix* Expedition. However, this is more likely due to differences in collection methods and depths than to a fundamental disparity in the hermit crab fauna of the areas. Prior to the *Alpha Helix* Expedition, 30 species of hermit crabs had been recorded from Maluku in 20 m or less (Table 2). Twenty-three species were known from Ambon, a major port of call since the 1500's and the place of origin of many collections which have been referred to in at least 15 publications. It is surprising that more has not been reported on the hermit crabs of Banda, as there have been Europeans there for about the same length of time as at Ambon: for several hundred years, under the Dutch East India Company, the Banda Islands were important in international trade as the major source of the world's nutmeg. However, in contrast to the 23 species from Ambon only three were previously recorded from Banda (see Introduction). Intensive collecting at Banda during the *Alpha Helix* Expedition yielded 35 species, all but one being new for the area. Additional species were being collected up to the last day of the expedition, and still more might have been taken had there been more time.

Twenty species were collected at Seram, 18 of them new records for that area. The total of 23 species known from Seram now equals the number recorded from Ambon. The 14 species collected at Saparua bring the total number from that area to 15, exceeding the 13 recorded from Ternate, the provenance of hermit crabs that were treated by at least seven authors. The 'Other' category in Table 2 includes a number of islands in Maluku from which shallow water paguroids have been reported; most of these records are by Buitendijk (1937) from the collections of the *Snellius* Expedition.

As shown in the table, 54 species of hermit crabs are now recorded from Maluku in depths of 20 m or less, with the *Alpha Helix* Expedition providing 24 new Moluccan records. These include seven new species: the four described in this paper, two species of *Pylopaguropsis* (McLaughlin & Haig, in press), and an undescribed species of *Calcinus*.

Fize & Serène (1955: v-ix), in their study of hermit crabs of Vietnam, described several types of environment in that area and listed the species (chiefly members of *Coenobita*, *Clibanarius* and *Dardanus*) that occurred in each. Placing our species from Maluku in the same environmental categories, we found considerable agreement with Fize & Serène's results – i.e. many of the same species occurred in the same environments in both geographical areas. Thus, by combining the data of Fize & Serène with those presented here it should be possible to predict some of the commoner species to be found in various shallow water habitats over a large part of South-east Asia.

Table 2. Hermit crabs known to occur in Maluku in depths of 20 metres or less (+ = species recorded in earlier literature; * = species from the *Alpha Helix* Expedition; SAPA. = Saparua; TERN. = Ternate)

	BANDA	SERAM	AMBON	SAPA.	TERN.	OTHER
<i>Birgus latro</i> (Linnaeus)	+	+	+	+	+	+
<i>Coenobita brevimanus</i> Dana	*		+		+	+
<i>Coenobita cavipes</i> Stimpson	*	+	+		+	+
<i>Coenobita perlatus</i> H. Milne Edw.	*		+			+
<i>Coenobita rugosus</i> H. Milne Edw.	*	+	+		+	+
<i>Coenobita spinosus</i> H. Milne Edw.			+			+
<i>Aniculus erythraeus</i> Forest	*					
<i>Aniculus retipes</i> Lewinsohn	*					
<i>Calcinus elegans</i> (H. Milne Edw.)	*			*		
<i>Calcinus gaimardii</i> (H. Milne Edw.)	*	*	+	*	+	+
<i>Calcinus guamensis</i> Wooster	*					
<i>Calcinus laevimanus</i> (Randall)	*		+			+
<i>Calcinus latens</i> (Randall)	*		+			+
<i>Calcinus minutus</i> Buitendijk	*	*				+
<i>Calcinus pulcher</i> Forest	*	*				
<i>Calcinus</i> sp. aff. <i>pulcher</i>	*	*				
<i>Clibanarius boschmai</i> Buitendijk				*		+
<i>Clibanarius corallinus</i> (H. Milne Edw.)	*		+			+
<i>Clibanarius cruentatus</i> (H. Milne Edw.)			+			+
<i>Clibanarius englaucus</i> Ball & Haig	*					
<i>Clibanarius eurysternus</i> (Hilg.)	*		+			+
<i>Clibanarius humilis</i> Dana			+			+
<i>Clibanarius laevimanus</i> Buitendijk						+
<i>Clibanarius longitarsus</i> (De Haan)		+	+		+	+
<i>Clibanarius merguensis</i> De Man			+		+	+
<i>Clibanarius padavensis</i> De Man						+
<i>Clibanarius striolatus</i> Dana			+			+
<i>Clibanarius virescens</i> (Krauss)	*		+			+
<i>Clibanarius zebra</i> Dana						+
<i>Dardanus deformis</i> (H. Milne Edw.)	+	+	+		+	+
<i>Dardanus gemmatus</i> (H. Milne Edw.)	*	*				
<i>Dardanus guttatus</i> (Olivier)	*	*	+	*	+	*
<i>Dardanus lagopodes</i> (Forskål)	*	*	+	*	+	+
<i>Dardanus megistos</i> (Herbst)	*	*	+	*	+	+
<i>Dardanus pedunculatus</i> (Herbst)	+	*	+	*		+
<i>Dardanus scutellatus</i> (H. Milne Edw.)						+
<i>Dardanus woodmasoni</i> (Alcock)	*					
<i>Diogenes avarus</i> Heller	*					
<i>Diogenes serenei</i> Forest	*					
<i>Diogenes viridis</i> n.sp.	*					
<i>Paguristes kuekenthali</i> De Man	*	*		*	+	
<i>Paguristes monoporos</i> Morgan	*	*				
<i>Paguristes runyanae</i> n.sp.	*					
<i>Trizopagurus strigatus</i> (Herbst)	*	*		*		
<i>Anapagrides</i> sp.				*		
<i>Anapagurus</i> sp.				*		
<i>Catapagurus ensifer</i> Henderson	*					
<i>Micropagurus vexatus</i> n.sp.	*	*		*		
<i>Pagurus hirtimanus</i> Miers	*	*	+		+	+
<i>Pagurus moluccensis</i> n.sp.	*					
<i>Pagurus pergranulatus</i> (Henderson)		*				
<i>Pylopaguropsis</i> sp. 1		*		*		
<i>Pylopaguropsis</i> sp. 2		*		*		
<i>Spiropagurus fimbriatus</i> Lewinsohn		*				
TOTAL SPECIES:	37	23	23	15	13	

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Glypturus motupore, a New Callianassid Shrimp (Crustacea: Decapoda) from Papua New Guinea with Notes on its Ecology

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ABSTRACT. A new callianassid shrimp, *Glypturus motupore*, is described from Papua New Guinea and compared with *G. acanthochirus*, *G. armatus* and *G. laurae*, three similar species of the genus from the Caribbean and Indo-West Pacific. *Glypturus motupore* is found intertidally and subtidally to depths of 30 m. The species processes large quantities of sediment and subtidally builds volcano-shaped mounds up to 46 cm high. Burrows are complex, extending up to 1.5 m deep and 2 m laterally. Burrows are lined with fine-grained sediments and include subsurface chambers accumulating coarse sediment.

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Only a single species of callianassid shrimp has been recorded from the nation of Papua New Guinea, *Callianassa novaebritanniae* Borradaile from the island of New Britain (De Man, 1928). However, De Man recorded 16 species from the family in the Indonesian archipelago. Three of these also occur in tropical Australia with two other species (Poore & Griffin, 1979). In addition, at least two undescribed species of callianassid shrimp are known from the Great Barrier Reef of Australia. It is probable therefore that the callianassid fauna of Papua New Guinea includes several species already described but the relatively abundant and newly discovered specimens described here could not be placed in a known species. This contribution describes the new species and provides some preliminary information about its ecology.

The diagnosis of this new species is based on that of the closely-related species *Glypturus laurae* (de Saint Laurent, in de Vaugelas & de Saint Laurent, 1984). The description follows the format used for several species in the family used by le Loeuff & Intes

(1974) and by de Saint Laurent & le Loeuff (1979). However, the generic placement of the new species differs from that of these authors who followed de Saint Laurent's (1973) concepts of callianassid genera. They included *G. laurae* and *G. armatus* (Milne Edwards) in *Callichirus* Stimpson. Manning & Felder (1986) have restricted *Callichirus* to *C. major* Say and three related species.

Manning (1987) revived and diagnosed *Glypturus* Stimpson for *G. acanthochirus* Stimpson and it is clear that our material can be assigned to this genus. Manning hesitated to include four other Indo-West Pacific species in *Glypturus*. They differ from the type species primarily in not having the anterolateral spines separated from the carapace by a non-calcified membrane. In a specimen from the Tuamotu Archipelago (nominally *G. armatus*) examined by GCBP the articulation was weak. The character would seem to be not important in the light of the many other similarities shared by this complex.

Type material is lodged in the Museum of Victoria, Melbourne (NMV), the Australian Museum, Sydney

(AM), the United States National Museum of Natural History, Washington (USNM), and the Muséum National d'Histoire Naturelle, Paris (MNHP).

CALLIANASSIDAE Dana

Glypturus Stimpson, 1866

Glypturus motupore n.sp.

Figs 1–3, 4a

Type material. HOLOTYPE: female, total length 134 mm, carapace length 38 mm, NMV J13811, Papua New Guinea, Bootless Inlet, Motupore Island (9°32'S, 147°16'E), intertidal sand flat north-east of University of Papua New Guinea's field station, collected by hand by T.H. Suchanek, June 1985, using the technique of de Vaugelas (1985). PARATYPES: male, tl. about 100 mm, cl. 29 mm, NMV J13812; female, tl. about 110 mm (damaged and incomplete), NMV J13813; female, tl. 104 mm, cl. 29 mm (no cheliped), NMV J13814; female, tl. 75 mm, cl. 22 mm (incomplete), NMV J13815; female, tl. 75 mm, cl. 22 mm; female, tl. 105 mm, cl. 29 mm, AM P37394; male, tl. 120 mm, cl. 34 mm (no cheliped), AM P37394; female, tl. 110 mm, cl. 30 mm, USNM 229516; male, tl. 82 mm, cl. 23 mm, USNM 229517; female, tl. 101 mm, cl. 21 mm, MNHP; all from type locality at different dates between 11 June and 28 July 1985.

Additional material examined. 3 unattached large chelipeds, 1 unattached smaller cheliped, same locality, NMV J13816.

Diagnosis. Cephalothorax a little less than 0.3 of total length. Cervical groove strongly marked, at 0.7 of carapace length. Front tridentate, rostrum and anterolateral spines not articulating. Telson lateral margins diverging over proximal half, with strongly convex posterior margin, about 1.2 times as wide as long. Propodus of maxilliped 3 broadly dilated, slightly excavate distally. Chelipeds unequal; larger armed with spines on lower margins of ischium, merus and carpus (proximal oblique row of 2–3 and distal longitudinal row of 3–7 on merus); spines on upper margins of merus and propodus; areas of granules laterally and mesially on merus. Uropodal endopod ovoid-triangular, twice as long as wide.

Description. Cephalothorax a little less than 0.3 of total length; relative lengths of cephalothorax, abdominal somites 1–6 and telson — 2.5 : 1.0 : 1.1 : 0.8 : 0.7 : 0.9 : 1.3 : 0.6. Rostrum acute, broadly based, upturned from base of eyes; anterolateral spines acute, fixed, slightly inwardly curved. Branchiostegite obscurely sculptured anteriorly. Abdominal somite 1 with clear shoulders. Telson about 1.2 times as wide as long, with diverging straight lateral margins over proximal half, almost semi-circular posterior margin, a central depression on distal half defined by broad longitudinal and transverse ridges.

Eyestalks tapering from base, cornea lateral, $\frac{3}{5}$ way along, apices rounded-triangular.

Antennule article 3 1.6 times length of article 2; flagella subequal, almost twice length of peduncle. Antenna peduncle exceeding antennule peduncle by its last article, article 5 shorter than article 4; flagellum twice as long as those of antennule.

Maxilliped 3 ischium 1.4 times as long as wide, crista dentata of 3 separate denticles proximally and a ridge of about 14 blunt denticles distally; merus about as long as greatest width; carpus longer than propodus and dactylus; propodus dilated, broader than long, distal margin slightly excavate. (See Fig. 3 for other mouthparts.)

Large cheliped (right in 6 cases, left in 5 cases) massive, as long as whole animal, without substantial sexual dimorphism. Ischium and merus of same length, carpus slightly shorter and propodus longer dorsally. Ischium with 8–11 spines on lower margin; merus with oblique row of 3 slightly curved spines proximally on lower margin, 3–6 (reducing distally) spines in longitudinal lower marginal row, 3 (rarely up to 8) spines on upper margin, lateral and mesial fields of granules; carpus with 6–11 distally-directed spines on lower margin, last 2 a distal pair; propodus with 3 spines on upper margin, rows of fine granules at base of dactylus, (6 scattered granules laterally at base of fixed finger only in AM P37394 female); fixed finger with blunt tooth on proximal half; dactylus longer than fixed finger, with proximal notch, blunt tooth, triangular notch and irregular cutting edge.

Small cheliped about $\frac{2}{3}$ length of larger. Ischium with about 12 denticles on lower margin; merus with 3 proximal and 2 distal spines on lower margin, 3 on upper margin; carpus with 6 spines on lower margin, last defining corner; propodus unarmed; fixed finger with proximal blunt tooth; dactylus simple.

Pereopod 3 propodus 2.3 times as broad as long, with strong narrow posterior lobe. Pereopod 4 propodus with short posterodistal finger, almost chelate. Pereopod 5 chelate.

Female pleopod 1 uniramous, 2 articles, second 1.4 times length of first. Pleopod 2 biramous, endopod with subterminal curved appendix interna, exopod shorter than endopod. Pleopod 3 biramous, endopod triangular, partly divided into 2 articles, triangular appendix interna; exopod curved and enclosing endopod.

Male pleopod 1 uniramous, 2 articles, second shorter than first, with distal curved acute lobe. Pleopod 2 biramous, endopod apex bilobed, one triangular, other truncate, cylindrical appendix interna; exopod shorter than endopod.

Uropodal endopod ovoid-triangular, twice as long as wide, widest about $\frac{1}{3}$ way along and tapering to rounded apex; exopod about as wide as long, anterior lobe obliquely truncate, posterior lobe broadly rounded, with proximal spine on rib.

Etymology. For Motupore Island, the type locality.

Distribution. Known only from Bootless Inlet, Papua New Guinea.

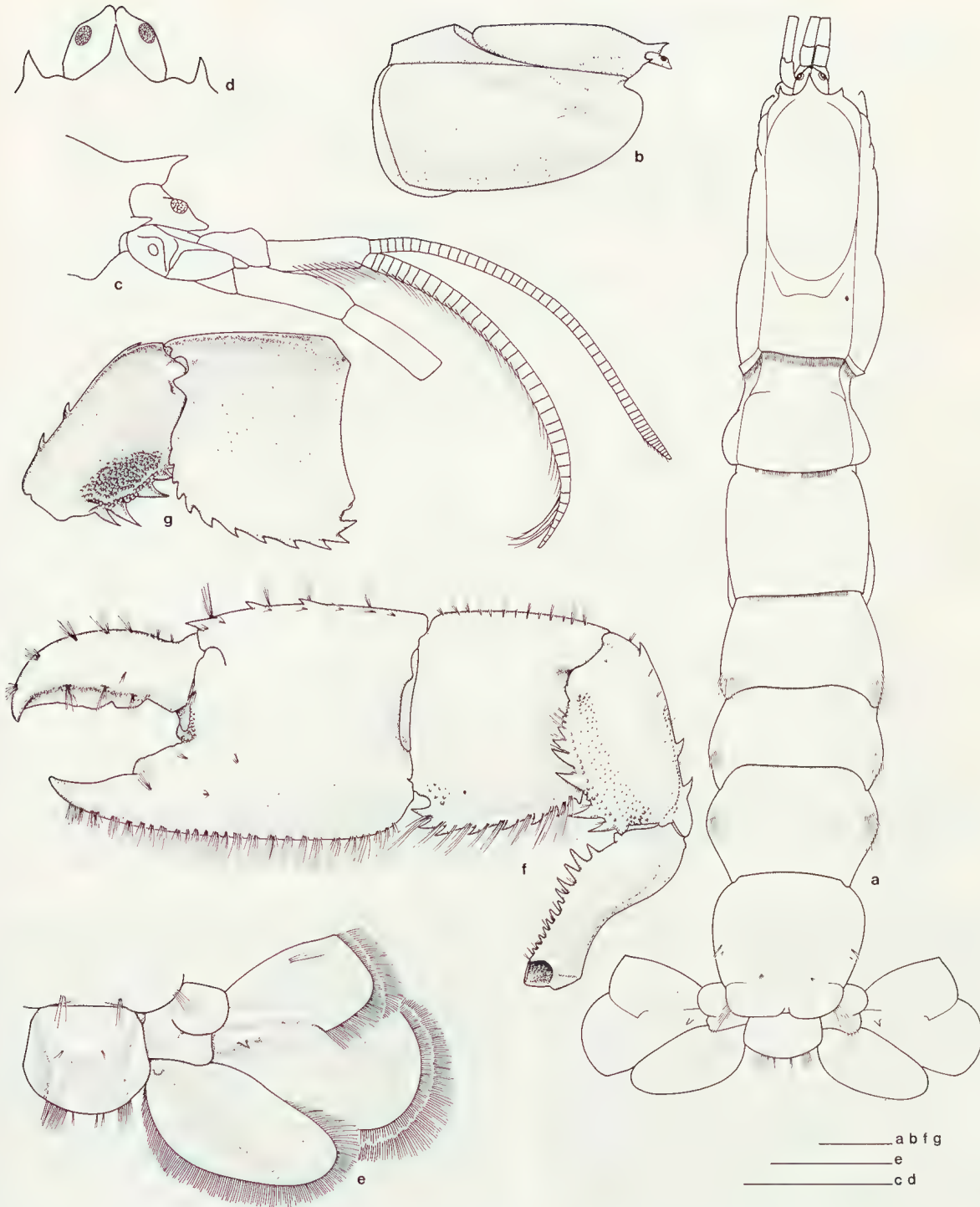


Fig.1. *Glypturus motupore* n.sp., holotype female: a, dorsal view (uropodal setae not shown); b, lateral view of cephalothorax; c, anterior section of cephalothorax, antennule and peduncle of antenna; d, anterior margin of cephalothorax and eyestalks; e, tailfan; f, larger right cheliped, mesial view; g, larger right cheliped merus and carpus, lateral view. (scale bars, 10 mm)

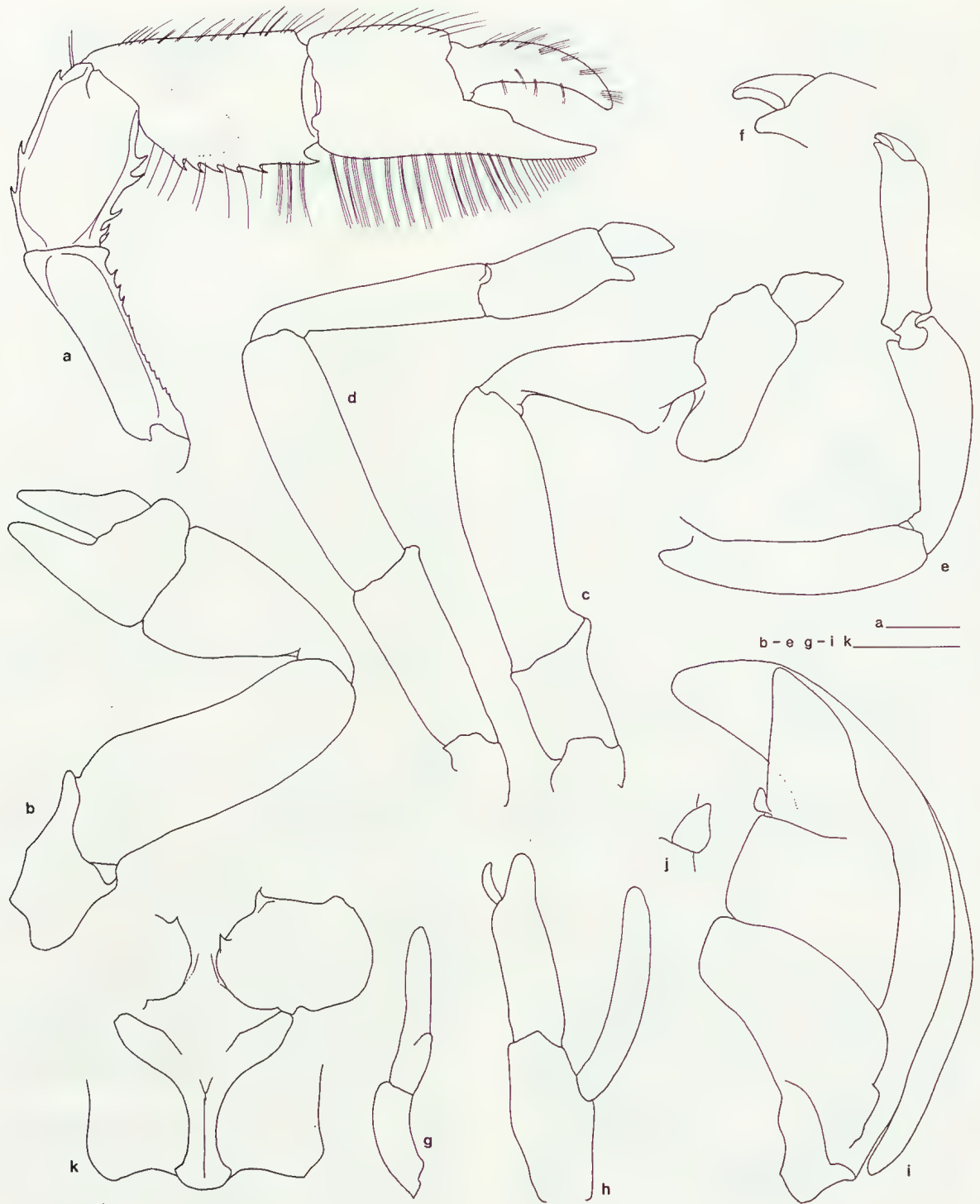


Fig.2. *Glypturus motupore* n.sp., holotype female: a, smaller left cheliped, mesial view; b-e, left pereopods 2-5; f, left pereopod 5 dactylus; g-i, left pleopods 1-3; j, pleopod 3 appendix interna, posterior view; k, sternal plate and coxa 4. (scale bars, 10 mm; setae shown only on a)



Fig.3. *Glypturus motupore* n.sp., holotype female: a, mandible; b, maxillule; c, maxilla; d-f, maxillipeds 1-3. Paratype male, NMV J13812: g,h, left pleopod 1 and detail of apex; i,j, left pleopod 2 and apex of endopod. (scale bars, 10 mm; setae not shown)

Taxonomic remarks. *Glypturus motupore* is closest to two other species from similar habitats in the Indo-West Pacific: *G. armatus* (Milne Edwards) described from Fiji and *G. laurae* (de Saint Laurent) from Aqaba, Red Sea; and to *G. acanthochirus* Stimpson from the Caribbean and south-eastern United States. A female of *G. armatus* (cl. 28 mm, MNHN Th. 656) from Mataiva, Tuamotu Archipelago; a female of *G. acanthochirus* (cl. 26 mm, USNM 122438) from Dry Tortugas, Florida; and a male of *G. laurae* (cl. 36 mm, NMV J11574) from the Gulf of Aqaba were used for comparison. Fig. 4 shows the important differences in the rostrum, eyestalks and tailfan. We do not agree with Manning (1987) who believed that *G. armatus* is a junior synonym of *G. acanthochirus*. The specimen of *G. acanthochirus* examined has the telson much more rounded posteriorly, and the uropodal endopod more acute. These observations are confirmed by Manning's (1987) and Biffar's (1971) figures.

Glypturus motupore shares with *G. armatus* and *G. acanthochirus* a similar elongate uropodal exopod

and the absence of granules on the propodus of the larger cheliped. It differs from *G. armatus* in the form of the uropodal exopod (slightly shorter in *G. armatus*), in the shape of the telson (of a more even width proximally in *G. armatus*), in the form of the rostrum (much narrower), in the eyestalks (broader, shorter and with larger cornea), and the greater number of ventral spines on the carpus (4-6 in *G. armatus*, 6-10 in *G. motupore*). *G. motupore* differs from *G. acanthochirus* in the shape of the telson (parallel-sided proximally in *G. acanthochirus*), uropodal endopod (wider proximally), and uropodal exopod (posterior section more square terminally).

Glypturus motupore shares with *G. laurae* a broadly-based upturned rostrum, tapering eyestalks with a small cornea but differs most importantly in the shape of the telson (narrower proximally in *G. motupore*), in the uropodal endopod (broader and more truncate in *G. laurae*), and the lobes of the uropodal exopod (anterior margin more curved and both slightly shorter in *G. laurae*). The larger chelipeds of the two species differ in the shape of the cutting edge of the dactylus (without a notch in *G.*

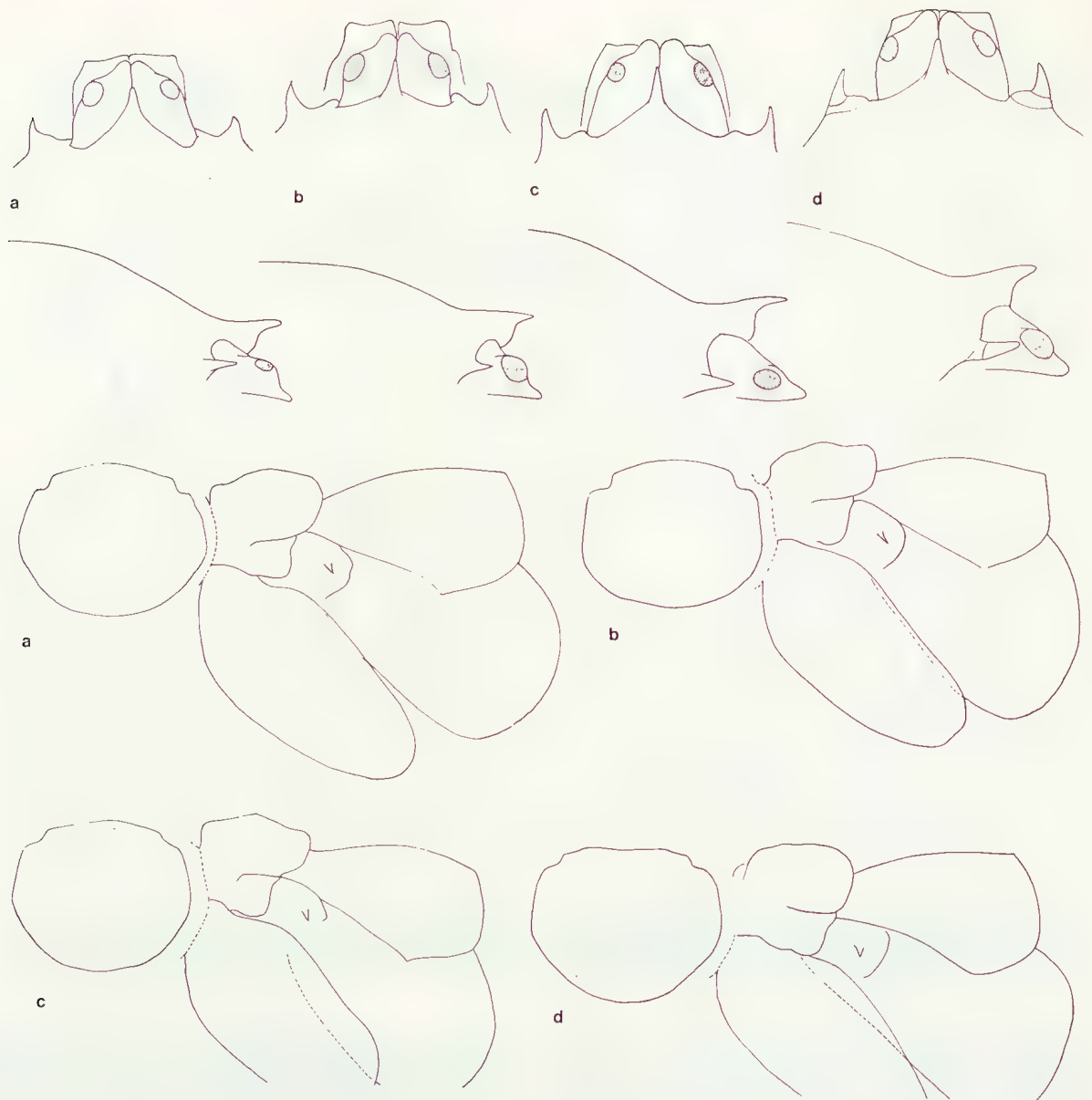


Fig.4. Rostrum, eyestalks and tailfan of four species of *Glypturus*. a, *G. motupore*, holotype, cl. 38 mm, Papua New Guinea, NMV J13811; b, *G. armatus*, cl. 28 mm, Taumotu, MNHN Th.656; c, *G. laurae*, cl. 35 mm, Aqaba, NMV J11574; d, *G. acanthochirus*, cl. 26 mm, Dry Tortugas, USNM 122438.

laurae), and in that lateral granules at the base of the fixed finger are absent in *G. motupore* (except in one individual) but are a constant prominent feature of *G. laurae*. The apex of pleopod 2 of the male is more rounded in *G. motupore* than in *G. laurae*.

A specimen from Mauritius described and figured by Kensley (1975) as *Callianassa armata* seems very similar to *G. motupore* especially in the shape of the telson and ornamentation of the large cheliped.

Distribution and Density

Glypturus motupore seems to be exceptionally catholic in its choice of habitats, being found both intertidally as well as subtidally in diverse conditions. Extensive populations, as evidenced by

their mound excavations, were found on intertidal sand flats on the northern (leeward) side of Motupore Island, Loloata Island and Manununa Island (also known as Lion Island). Dense populations were also found subtidally to 30 m depth on fine sandy bottoms throughout most of Bootless Inlet (Table 1.) On and around Motupore Island, mounds were also found in mostly subtidal (but occasionally intertidal habitats occupied by seagrasses (e.g., *Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea rotundata*, *Halophila ovalis* and *Halodule uninervis*).

Behaviour Patterns

SEDIMENT PROCESSING. This species processes large volumes of carbonate sediment in a manner

Table 1. Population density of *Glypturus motupore* as estimated by mound densities.

Habitat	Mean mound density (per m ²)	Mean maximum mound height (cm)	Range of maximum height (cm)	Number of 1 m ² quadrats
Subtidal (20 m) sand flats (Manununa Island)	2.36±1.40	19.13±8.89	5–46	39
Subtidal (c. 6 m) grass beds (north-east Manununa Island)	1.29±1.17	11.13±3.72	5–17	63
Intertidal sand flats (north-east Motupore Island)	1.55±1.20	n/a	n/a	60

apparently similar to other tropical thalassinidean shrimps studied to date (Suchanek, 1985). Sediment is drawn into the burrow system partially by gravity by opening one or more intake pits located at the sediment/water interface. Sand grains are then presumably gleaned to remove organic detritus. After removal of organics, fine-grained sediments are pumped (with the aid of pleopodal currents) to the surface. Subtidally, ejected sediments form volcano-shaped mounds ranging up to at least 46 cm in height. Sediment processing continues day and night, with 24-hour pumping rates of c. 200–400 ml of sediment per mound.

GRASS PULLING. In addition to drawing sediment into the burrow system, the species has been seen to pull seagrass blades into the burrow via the intake pits. It is not known whether it feeds directly on seagrass detritus as does *Upogebia affinis* (Pearse, 1945). Alternatively, it may store these blades in subsurface chambers and cultivate bacteria or fungi on which to feed at a later date (see Braithwaite & Talbot, 1972; Frey & Howard, 1975; Ott *et al.*, 1976; and Suchanek, 1985 for discussion).

Burrow Characteristics

PHYSICAL COMPLEXITY. The burrow system of this species is especially complex. Suchanek *et al.* (in prep.) will show a photograph of a burrow resin cast. From both resin casting and grass-feeding experiments, burrows were found to extend 1.5 m or more below the sediment surface. From resin casts and dye experiments for lateral connectedness, large burrows were found to extend at least 2 m laterally. Most burrows had typical sediment surface openings (the bottom opening of intake pits) ranging from 11–23 mm in diameter. Dimensions for typical internal diameters of subsurface burrows (from one large burrow resin cast) ranged from 23–26 mm, with many enlarged turnaround sites (up to 54 X 74 mm), and several “refuse” chambers up to 220 X 170 mm (see Suchanek *et al.* (in prep.) for details). Although never captured, thalassinidean shrimps from Enewetak Atoll show very similar mound excavations and burrow structures as evidenced by

resin casting techniques (Suchanek *et al.*, 1986).

INTAKE PITS. The burrow system typically has 1–3 (or more) funnel-shaped intake pits through which surface sediments (and/or seagrass blades) are drawn into the burrow.

MOUNDS. Typically at least 3–4 volcano-shaped mounds are associated with each burrow system. The burrow lining that passes out through the mounds is typically very thin and non-compacted.

BURROW LINING. The burrow lining is approximately 8–15 mm in thickness and is composed internally (the portion facing the inside of the burrow) of compacted fine-grained sediments and externally (the portion in communication with the surrounding sediments) of coarse-grained particles (coral fragments and shell debris). No grass was found incorporated into burrow lining.

SUBSURFACE REFUSE CHAMBERS. Subsurface burrow chambers are numerous and complex and accumulate coarse-grained sediments (similar to those found in burrow systems of Caribbean *Callianassa rathbunae* by Suchanek, 1983). No grass-filled chambers were found.

ACKNOWLEDGEMENTS. We are grateful for the help and cooperation of the staff of the Motupore Island Research Department, University of Papua New Guinea, especially Dr Patrick Colin, Ignacious Taliana, Sae Gwae, Moses Kollowan and Dr Nicholas Polunin. We are also deeply indebted to 18 Earthwatch divers, without whose dedication and support this project could never have been completed.

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Balanoid Barnacles of the Genus *Hexaminius* (Archaeobalanidae: Elminiinae) from Mangroves of New South Wales, including a Description of a New Species.

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ABSTRACT. *Hexaminius foliorum* n.sp. is described and separated from *H. popeiana* Foster on differences in adult and larval anatomy, supported by differences in cirral activity, copulatory activity and breeding. Structure, function and reproduction in *H. foliorum* are more specialised than in *H. popeiana*. The differences are related adaptively to the occupancy by *H. popeiana* of a variety of hard substrata, but not mangrove leaves, and the confinement of *H. foliorum* to the ephemeral habitat of immersible mangrove leaves. *Hexaminius foliorum* may be a specialised descendant of *H. popeiana*.

ANDERSON, D.T., J.T. ANDERSON & E.A. EGAN, 1988. Balanoid barnacles of the genus *Hexaminius* (Archaeobalanidae: Elminiinae) from mangroves of New South Wales, including a description of a new species. Records of the Australian Museum 40(4): 205–223.

Foster (1982) revised the taxonomy of the high shore estuarine barnacles of New South Wales, hitherto referred to as *Elminius modestus* Darwin (Pope, 1945). The majority of the four-plated specimens were referred by Foster to a new species, *Elminius covertus*. Foster also observed that *E. covertus* is intermingled with a six-plated archaeobalanid which he described and named as *Hexaminius popeiana*. An archaeobalanid subfamily Elminiinae was erected by Foster in recognition of the close relationship between *Hexaminius* and *Elminius*, a concept further supported by Buckeridge (1983) and by Egan & Anderson (1985), who described the larval development of *H. popeiana* and *E. covertus*. The larvae of *E. covertus* are close to but different from those of *E. modestus*. The larvae described by Egan & Anderson (1985) under the name *H. popeiana* are more like those of the *Conopea* group of archaeobalanines, but also share sufficient features in common with the larvae of *Elminius* to lend further weight to the Elminiinae as a distinct subfamily.

During their study of larval development, Egan and Anderson noted that *H. popeiana* were to be

found at their study site (Iron Cove, Port Jackson, NSW) on two distinct surfaces, rocks and the lower leaves of the mangrove *Avicennia marina*. The settlement of this species on mangrove leaves was not mentioned by Foster (1982), nor, indeed has this part of the mangrove surface been recorded as a habitat for other balanomorphs in Australia, although a number of species are known to inhabit mangrove trunks and pneumatophores (Hutchings & Recher, 1982; Achituv, 1984). The observation was therefore of sufficient interest to prompt Egan and Anderson to make parallel studies during 1982–1984 of the seasonal breeding of populations of *H. popeiana* from rocks and mangrove leaves at the Iron Cove site, while utilising the mangrove leaf individuals as a source of nauplii for larval culture. Initially it was assumed that the differences in external appearance between the mangrove leaf and rock populations were a consequence of a greater level of erosion of the rock-dwelling individuals. However, a study of seasonal cycles during 1982–1984 showed that the two populations had different breeding patterns. The mangrove leaf population, as illustrated by Egan & Anderson (1985), bred throughout the year, with

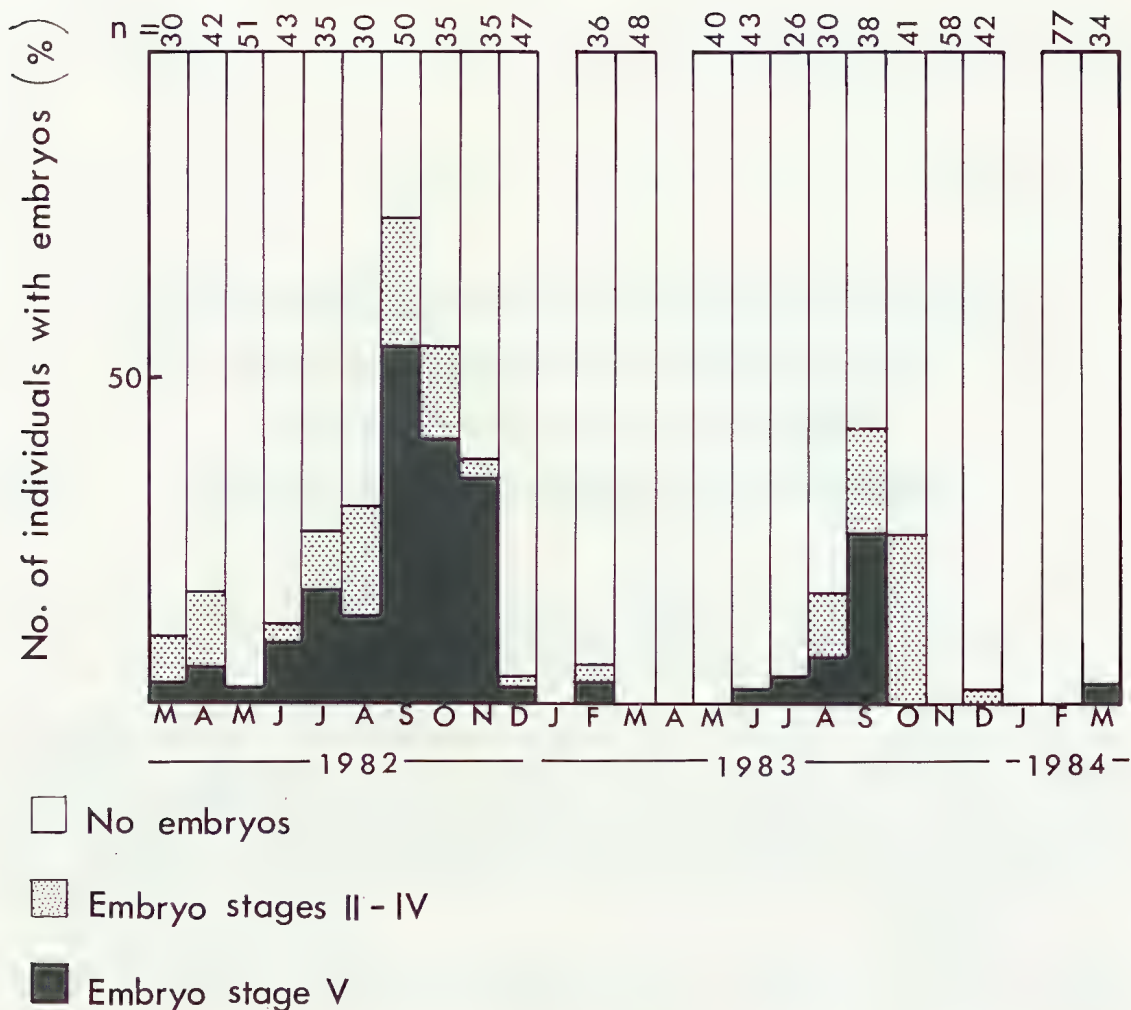


Fig.1. Percentages of individuals of rock-dwelling *Hexaminius popeiana* brooding embryos of different developmental stages, in monthly samples from Iron Cove, Port Jackson, NSW from 1982 to 1984. Sample size is given at the top of each column. The embryo stages are those of Sandison (1954).

some reduction in the autumn months. The rock population, in contrast, built up through the winter to a spring breeding peak, and showed little or no breeding during the summer and autumn (Fig. 1).

The question therefore arose, whether the external differences between the leaf-dwelling and rock-dwelling animals were indicative of separate breeding populations. We have now made a thorough morphological comparison of animals from the two substrata, utilising animals from a number of sites along the New South Wales coast, some of which were also used as collection sites by Foster (1982). In view of the apparent association of one of our breeding populations with the leaves of *Avicennia marina*, we took particular care also to collect specimens from the trunks of mangroves as well as from the leaves, and from rock surfaces in each locality.

This comparison has shown that there are two species of *Hexaminius* in the estuaries of the central coast of New South Wales. One of them, referable to

H. popeiana Foster, inhabits surfaces of a permanent or semipermanent nature on the upper shore of sheltered estuarine locations, including rocks, wooden structures and the trunks of mangrove bushes. The other species, newly described here, is confined to the leaves of *Avicennia marina*. Much of the present paper is devoted to a description of the new species. We also provide a more extended description of *H. popeiana* than was given by Foster (1982). Many of the features which differ between the two species were not mentioned in the initial description by Foster.

The description of the larval stages of *H. popeiana* given by Egan & Anderson (1985) was based on larvae obtained from mangrove leaf populations, and is therefore referable to the new species. As supplementary evidence of the differences between the species, we include in this paper a comparative account of the larvae of *H. popeiana* (s.s.), which are similar in general but different in detail from those of *H. n. sp.* We conclude our account with an analysis of

the cirral activities and copulatory activities of *H. popeiana* and *H. n. sp.* These activities also differ in ways that support the morphological analysis.

Materials and Methods

All specimens used for anatomical studies were collected in August and September 1984, at the height of the breeding season for *H. popeiana* and within the long period of maximum breeding activity of *H. n.sp.* All specimens were therefore sexually mature. Observations on cirral activity and copulatory activity (see below) were also made at the time. Larval cultures of *H. popeiana* (see below) were reared in August and September 1984.

Thirty individuals of each species, collected from Iron Cove, NSW, were investigated anatomically by the dissection of fresh specimens and specimens preserved in 5% formalin in seawater (V/V). Limbs and mouthparts were mounted in polyvinyl lactophenol after staining in lignin pink. Wall plates and opercular plates were disarticulated and cleared using sodium hypochlorite. Podomere counts were made for all limbs.

During or subsequent to each dissection, measurements were taken as follows: basal length and width; orifice length and width; scutum length (along occludent margin) and height (from occludent margin to basitergal angle); tergum length (from apex to tip of spur) and width (from scutal margin to carinobasal angle); ramal length for cirri III, IV–VI; length (from second tooth to base) and width (across cutting edge) of the mandible; length (from middle of cutting edge to base) and width (across cutting edge) of the maxillule; length (from base to tip) and width of the maxilla. These measurements were used to calculate the various ratios given in the results.

The larvae of *H. popeiana* described in this paper were reared and studied by the methods of Egan & Anderson (1985). Gravid specimens collected from Iron Cove and Folly Point, Port Jackson, NSW were used as a source of stage I larvae.

Cirral activity and copulatory activity were analysed from videotape records. Animals were filmed using a Sony video camera fitted with a Vivitar 90 mm macrolens, and a Sony U-matic portable videorecorder. Freshly collected animals were immersed in seawater at 23–25°C in a small perspex tank and illuminated by a Volpi fibre-optic lamp. Numerous sequences of cirral activity and copulatory activity were recorded and compared. Only general features of these activities are reported here. A detailed analysis will be presented elsewhere.

Hexaminus foliorum n.sp.

Figs 2–4

Hexaminus popeiana.—Egan & Anderson, 1985: 383.

Type material. HOLOTYPE hermaphrodite, 7.0 mm basal length, sexually mature, AM P37462 (spec. D26, Fig. 2a,

complete shell 190). PARATYPES hermaphrodite, sexually mature, AM P (spec. D25, Fig. 2e, coll. 14 May 1984, 189), from Sisters Bay, Iron Cove, NSW, 33°51.5'S 151°09.5'E, on leaves of *Avicennia marina*, collected by D.T. Anderson, Aug 1984.

Additional material examined. Part specimens: DA bleached plates (Fig. 2b,c,d), 212; body (Fig. 2f), 59; spec. D1, oral cone (Fig. 4a), 54A; labrum (Fig. 4b), 65; DB penis (Fig. 4g), 217. Slides: cirri I–VI, D22, 13 May 1983, right cirri, 85; spec. D5, right palp and right mandible (Fig. 4c,d), 19; spec. D5, left maxillule and left maxilla (fig. 4e,f), 17. *Hexaminus foliorum* was also collected from the lower (immersion) leaves of *Avicennia marina* at Gosford and Woy Woy, on Brisbane Waters, and at Hawks Nest, Port Stephens; all localities on the Central Coast of NSW between 33–34°S.

Diagnosis. *Hexaminus* of low conical form; basal margin ovoid with bluntly protruding ribs; conspicuous reddish brown radial bands externally. Wall plates and opercular plates thin, fragile. Wall plates with thin basal margins; basis membranous, thick, semiopaque. Tergoscutal flaps with shallow carinal fold. Scutal depressor muscles thin. Prosoma elongate, fusiform; cirri IV–VI with long rami and long setae. Pedicel of penis not enlarged.

Description. The following description is based on 30 additional specimens from Iron Cove, NSW, which were destroyed during the course of the study.

EXTERNALS. Shell (Fig. 2a) to 7.0 mm in rostracarinal basal length, low conical, even when crowded; basal length markedly greater than width, basal margin ovoid. Colour when live, pale brown, with darker reddish brown radial bands between low ribs. Preserved, cream with brown radial bands. Growth lines with conspicuous white spines. Ribs protruding bluntly around basal margin.

WALL. 6 plates, thin, fragile; rostrum (Fig. 2b) large, ovoid; carinolaterals narrow, width about 1/2 of laterals; radii moderate, leaving part of alae exposed.

ORIFICE. Pentagonal, width about 3/4 length; rostral side short, straight.

OPERCULUM. Colour when live, brown, with white patches at rostral and lateral scutal angles; lateral patches extend toward apex as less conspicuous, whitish chevron. Preserved, greyish brown with whitish chevron on tergal edges of scuta. Opercular membrane pale brown. Tergoscutal flaps not deeply folded carinally; live, beige with cream edges, paired dark brown patches centrally, paired pale brown patches rostrally. Preserved, pale brown with cream edges; paired dark brown patches centrally.

BASIS. Membranous, thickish, semiopaque; ovaries creamy white to yellowish.

INTERIOR OF WALL. Mantle cream to brownish purple, dark brown beneath operculum. Exposed inner surfaces of wall plates cream, with reddish brown radial bands; basal margins (Fig. 2e) thin, sharp, sometimes with slight development of radial teeth. From basal margin to perimeter of sheath, internal surface of parietes gently sloping, not conspicuously hollowed out.

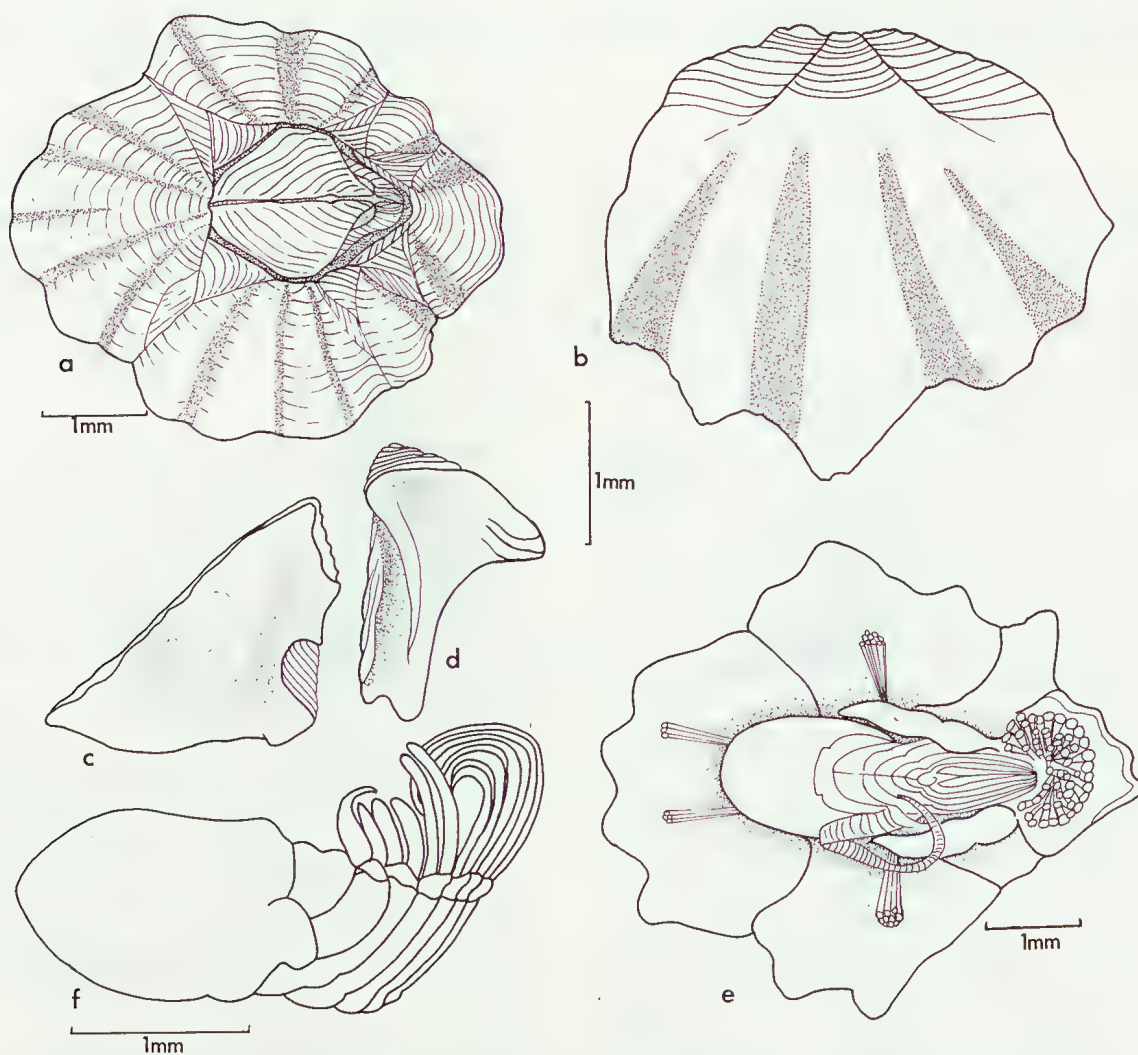


Fig.2. *Hexaminius foliorum*. a, apical view; b, rostrum, internal view; c, left scutum, internal view; d, left tergum, internal view; e, basal view with basis removed; f, body and limbs in right lateral view.

OPERCULAR PLATES. Thin, translucent, like wall plates. Scutum (Fig. 2c) slightly longer than high; articular ridge and furrow of approximately equal length, articular furrow shallow; adductor scar faint; depressor muscle scars very faint or absent. Tergum (Fig. 2d) hatchet shaped, frequently narrow; articular margin straight, with shallow articular furrow; basal margin straight, except apically, where it curves to join occludent margin as projection bearing 3–4 prominent muscle crests; tergal spur close to but separate from basiscutal angle, forming an acute angle with the short part of the basal margin and merging into the straight longer part of this margin; spur longer than basiscutal angle, concave internally.

OPERCULAR DEPRESSOR MUSCLES. Cloudy white in fresh specimens, brown when preserved. Tergal depressors (Fig. 2e) large, with distinct, large fibres; lateral scutal depressors thin; rostral scutal depressors very thin.

BODY. Prosoma (Fig. 2e,f) elongate and fusiform; postprosomal leg bases in paired linear array. Protopod of cirrus I just overlapping oral cone; protopods of II and III more posterior.

BRANCHIAE. Long, moderately wide (Fig. 2e), thin, smooth, semiopaque, white.

CIRRI. Cirrus I (Fig. 3a). Exopod, with 12–15 podomeres, half as long again as endopod; proximal podomeres of exopod broad, with setal bunches directed posteriorly; distal podomeres narrow, with setae directed apically. Endopod, with 6–7 podomeres, broad throughout; podomeres with anteriomedian cushions bearing bunches of anteroapically directed setae, some stout. Coxal setae pappose, other setae serrulate.

Cirrus II (Fig. 3b). Rami subequal, endopod slightly the longer; podomere numbers 8–9 and 7–10; both rami broad, tapering, with setae dense, anteriorly pointing, serrulate. Coxal setae pappose.

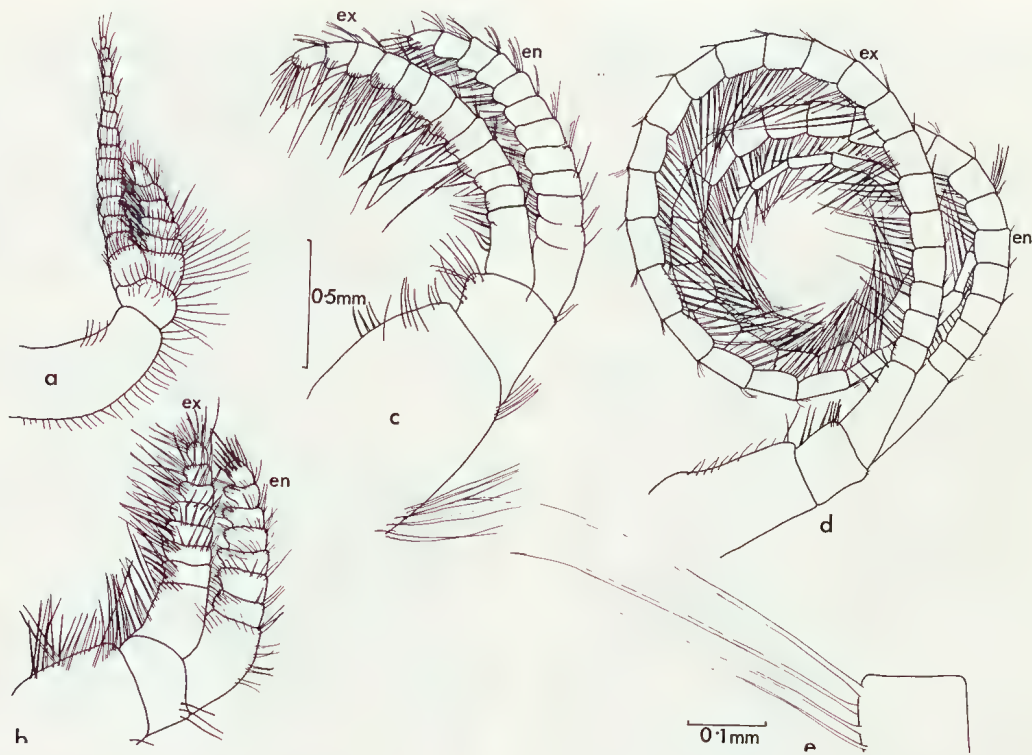


Fig.3. *Hexaminus foliorum*. a, cirrus I left, median view; b, cirrus II right, lateral view; c, cirrus III right, lateral view; d, cirrus V right, lateral view; e, podomere of endopod of cirrus V; en, endopod; ex, exopod.

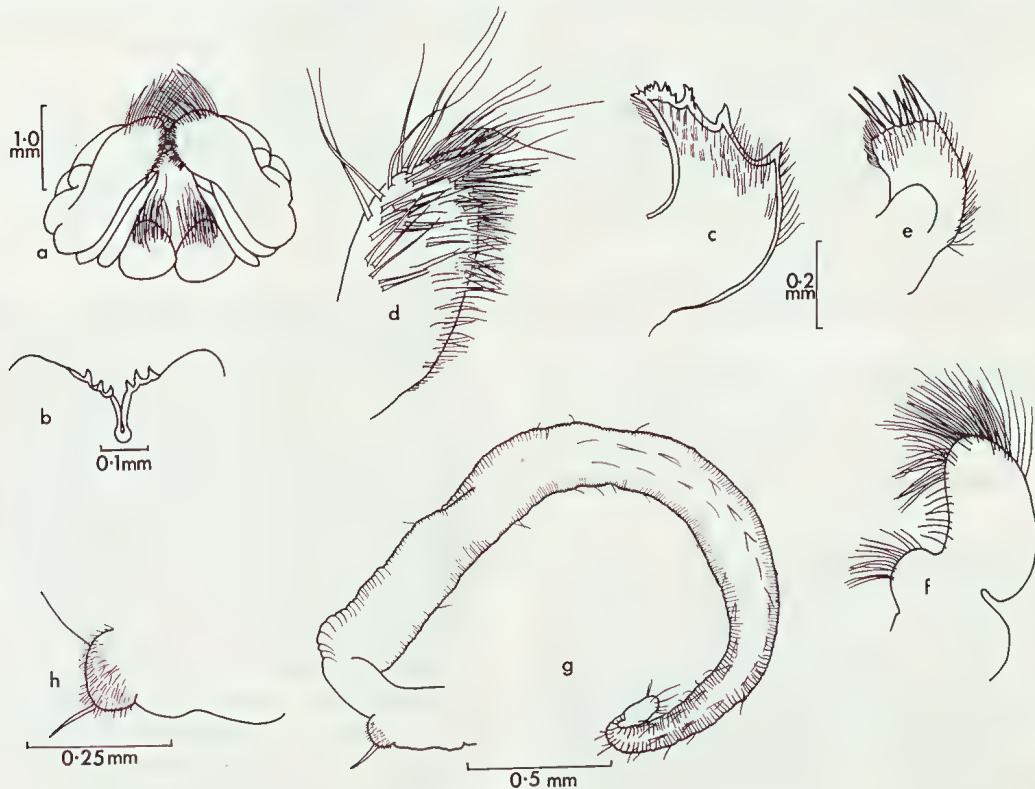


Fig.4. *Hexaminus foliorum*. a, oral cone in posterior view; b, labrum; c-f, mouthparts of right side; c, mandible; d, mandibular palp; e, maxillule; f, maxilla; g, penis in left lateral view; h, basidorsal point of penis.

Cirrus III (Fig. 3c). Rami equal, cylindrical, podomere numbers 11–13 and 10–12; mixed serrate and serrulate setae pointing anteriorly. Coxal setae pappose.

Cirri IV–VI (Figs 3d,e). Rami equal, 2.4, 3.4 and 3.8 times as long as those of cirrus III; podomere numbers 18–25 (IV), 23–29 (V) and 25–30 (VI). Anterolateral setae, 2 pairs per podomere proximally to 7 pairs distally, some reduction apically. Setae very long relative to ramal length. Protopods and rami slender.

MOUTHPARTS. Oral cone (Fig. 4a) slightly broader than high in posterior view, with palps set obliquely and conspicuous maxillae projecting posteriorly. Labrum (Fig. 4b) deeply notched, with 3 prominent teeth on either side. Mandible (Fig. 4c) quadridentoid, broad, ratio of length to width 0.98; incisor tooth separated from second tooth by half length of cutting edge; second to fourth teeth with subsidiary cusps; fourth tooth close to molar process. Molar process blunt, with low teeth, the first larger than the remainder; distal surfaces of mandible setose, setae set in palmate groups. Palp (Fig. 4d) with median edge straight, apex steeply convex. Apical fringe of long serrulate setae, median fringe of evenly spaced, short, jointed setae. Maxillule (Fig. 4f) long and narrow, ratio of length to width 1.7; with 2 spines at lateral angle, slight notch followed by 3 shorter and 2 longer spines; median angle with 4 pairs of small spines. Fringe of setae along almost entire lateral edge. Maxilla about half as broad as long, with dome-shaped end; apical setae long, fine serrulate; distoventral setae shorter, serrulate; proximoventral setae short, jointed, densely packed.

PENIS (Fig. 4g). Long, annulated throughout; pedicel little greater in diameter than base of penis, clothed in short spines; small basidorsal protuberance (Fig. 4h) covered with short setae, bearing 0, 1 or 2 longer, serrulate spines.

Etymology. Noun in apposition (*L. folium* = leaf), named after habitat: leaves on mangrove, *Avicennia marina*.

Distribution. Estuaries of central coast of New South Wales.

Hexaminus popeiana Foster

Figs 5–7

Hexaminus popeiana Foster, 1982: 28.

Not *Hexaminus popeiana*.—Egan & Anderson, 1982: 383 (= *H. foliorum*).

Material examined. Whole specimen: body in shell showing gills and muscles (Fig. 5a,e), 90. Part specimen: EA bleached plates (Fig. 5b–d), 206; spec. E12, whole body (Fig. 5f), 114; spec. E11, oral cone (Fig. 7a), 99; labrum (Fig. 7b), 117; EA penis (Fig. 7g), 208. Slides: spec. E6, right cirri I (Fig. 6a), right cirri II (Fig. 6b); spec. E6, right cirri III (Fig. 6c), right cirri IV; spec. E6, right cirri V (Fig. 6d,e), right cirri VI; spec. E6, left palp (Fig. 7c), left mandible (Fig. 7d); spec. E6, left maxillule (Fig. 7e), left

maxilla (Fig. 7f). *Hexaminus popeiana* was collected from rocks and jetsam, wooden structures and the trunks and branches of *Avicennia marina* at Iron Cove (AM P37464), Rose Bay, Vacluse and Folly Point, Port Jackson, NSW; Taren Point, NSW; Nelson Bay, Lemon Tree Passage, Tanilba Bay and Karuah, Port Stephens, NSW; all between lat. 33°–34°S; and at Magnetic Island, north Qld, lat. 19°S, long. 147°E. The latter is a first record of the species beyond the coast of New South Wales and indicates a distribution of *H. popeiana* in estuaries along a major part of the coast of eastern Australia.

Diagnosis. Conical form; basal margin circular, lacking protruding ribs; reddish brown radial bands weak or absent. Wall plates and opercular plates thick, heavy. Wall plates with broad basal margins; basis membranous, thin, transparent. Tergoscutal flaps with deep carinal fold. Scutal depressor muscles thick. Prosoma short and round; cirri IV–VI of moderate length, with moderate length setae. Pedicel of penis enlarged.

Description. In this section we draw attention to those anatomical features in which *H. popeiana* (s.s.) differs from *H. foliorum*. The description is based on 30 specimens taken from rocks at Iron Cove, NSW.

EXTERNALS. Shell (Fig. 5a) up to 10.2 mm in rostracarinal basal length, conical, tall when crowded; basal length only slightly greater than width, basal margin almost circular. Colour when live, greyish cream, uneroded specimens with darker radial bands between broad, low ribs. Preserved, grey. Growth lines in uneroded specimens with small white spines. Basal margin smooth to irregular, ribs not protruding.

WALL. 6 plates, solid and heavy; rostrum (Fig. 5b) large, squareish; carinolaterals narrow, width about $\frac{1}{4}$ of laterals; carina narrow, width about $\frac{1}{3}$ of rostrum; radii moderate, leaving part of alae exposed.

ORIFICE. Pentagonal, width about $\frac{3}{4}$ length; rostral side concave.

OPERCULUM. Colour when live, purple brown, with conspicuous white chevron on tergal edges of scuta. Preserved, greyish brown, with white chevron unless eroded. Opercular membrane midbrown. Tergoscutal flaps deeply folded carinally; live, pale cream with white edges; with paired, very small, dark brown patches centrally and paired, dark brown patches rostrally and tergally, the latter pair deep within the tergal folds of the flaps; preserved, pale brown with cream edges, paired dark brown patches centrally and rostrally.

BASIS. Membranous, thin, transparent; ovaries creamy white to yellowish.

INTERIOR OF WALL. Mantle dark purple with brown edge marginally, dark brown beneath operculum. Exposed inner surface of wall plates pinkish mauve, becoming whitish when preserved; basal margins (Fig. 5e) flattened, broad, sometimes with single row of small radial teeth. From basal margin to perimeter of sheath, surface of parietes

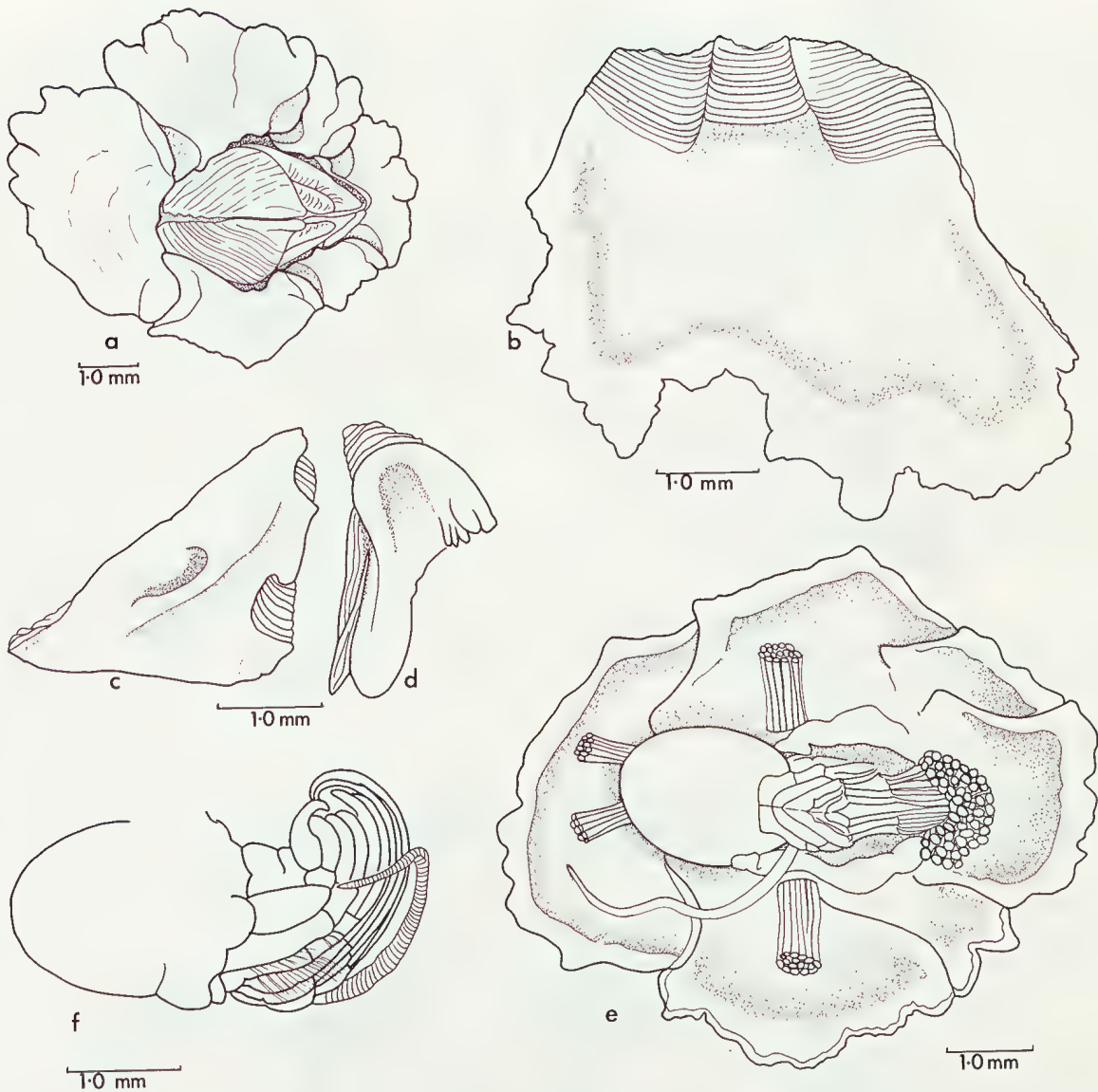


Fig. 5. *Hexaminius popeiana*. a, apical view; b, rostrum, internal view; c, left scutum, internal view; d, left tergum, internal view; e, basal view with basis removed; f, body and limbs in right lateral view.

concave, conspicuously hollowed out.

OPERCULAR PLATES. Thick, opaque, like wall plates. Scutum (Fig. 5c) longer than high; articular ridge long, articular furrow short and deep; adductor ridge faint or absent; depressor muscle scars very faint or absent. Tergum (Fig. 5d) with occludent margin broad and obvious in apical view; club shaped, frequently broad; articular margin straight, with deep articular furrow; basal margin concave, curving apically to join occludent margin as projection bearing 4–5 irregular muscle crests; tergal spur located as in *H. foliorum* but not longer than basiscutal angle, flat internally.

OPERCULAR DEPRESSOR MUSCLES. Translucent white in fresh specimens, brown when preserved. Tergal depressors large (Fig. 5e), lateral scutal depressors moderately large, rostral scutal depressors thin.

BODY. Prosoma rounded, broad (Fig. 5e,f); postprosomal leg bases compacted together and overlapping. Protopods of cirri I–III curved around oral cone.

BRANCHIAE. As in *H. foliorum* but translucent white.

CIRRI. Cirrus I (Fig. 6a). As in *H. foliorum* but exopod nearly twice as long as endopod; podomere numbers 13–18 and 6–7; setae of endopod cushions a mixture of serrate, serrulate and simple. Coxal setae mixed pappose and serrulate.

Cirrus II (Fig. 6b). As in *H. foliorum* but rami slightly longer, podomere numbers 8–10 and 8–11.

Cirrus III (Fig. 6c). As in *H. foliorum*.

Cirri IV–VI (Fig. 6d,e). Rami equal, 2.4, 2.9 and 3.6 times as long as those of cirrus III, thus relatively shorter than in *H. foliorum*; podomere numbers 16–22 (IV), 21–25 (V) and 19–27 (VI). Anterolateral

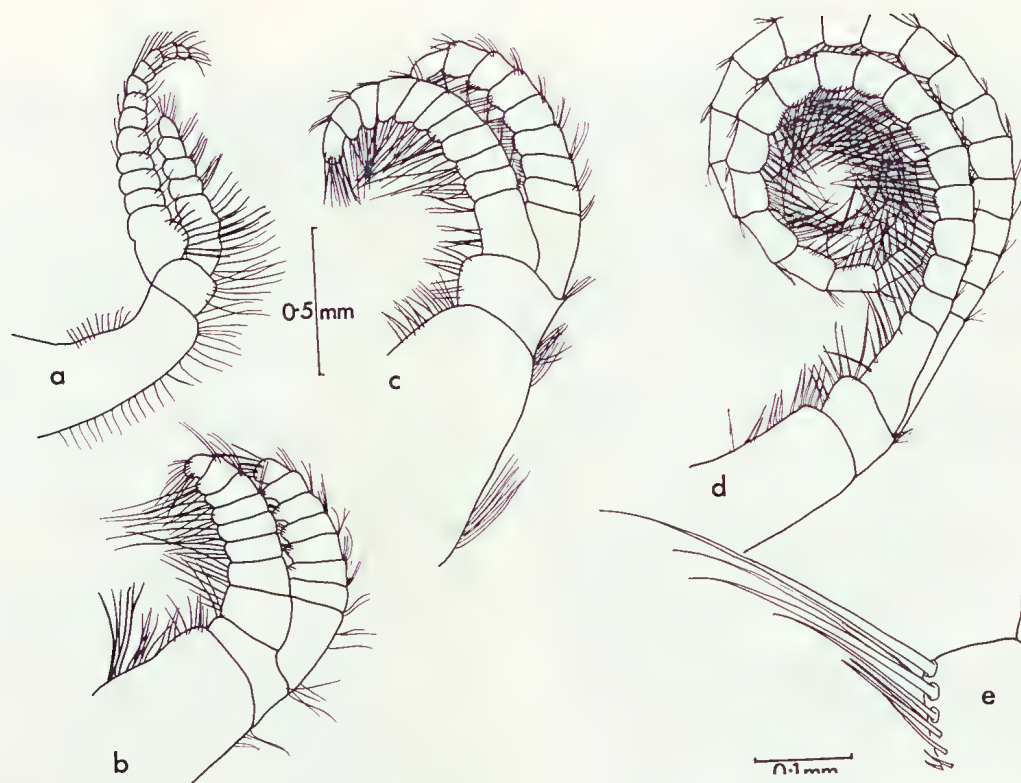


Fig. 6. *Hexaminius popeiana*. a, cirrus I left, median view; b, cirrus II right, lateral view; c, cirrus III right, lateral view; d, cirrus V right, lateral view; e, podomere of endopod of cirrus V.

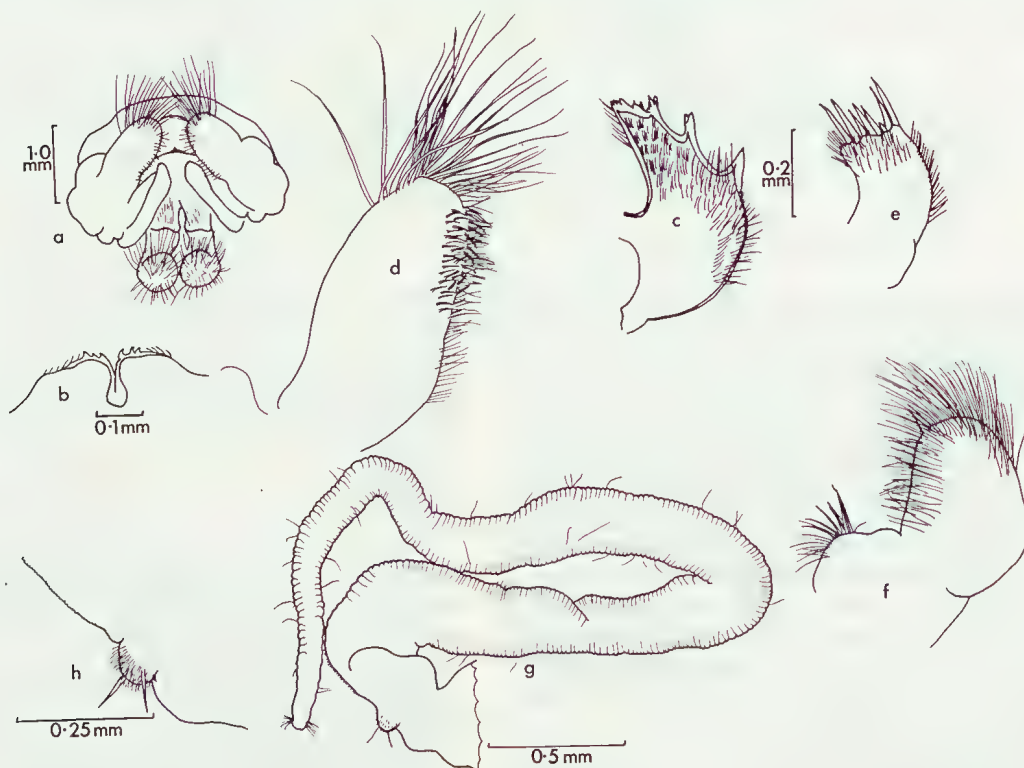


Fig. 7. *Hexaminius popeiana*. a, oral cone in posterior view; b, labrum; c-f, mouthparts of right side; c, mandible; d, mandibular palp; e, maxillule; f, maxilla; g, penis in left lateral view; h, basidorsal point of penis.

setae 2 pairs per podomere proximally to 8 pairs distally, some reduction apically. Setae long relative to ramal length. Protopods and rami quite stout.

MOUTHPARTS. Oral cone (Fig. 7a) as in *H. foliorum* but teeth small. Labrum (Fig. 7b) as in *H. foliorum*. Mandible (Fig. 7c) as in *H. foliorum*, but narrower, ratio of length to width 1.42. Palp (Fig. 7d) as in *H. foliorum*, but apex roundly convex, median fringe of short, jointed setae massed towards apex. Maxillule (Fig. 7e) as in *H. foliorum*, but broader, ratio to length to width 1.3; median angle with 2 pairs of small spines. Maxilla (Fig. 7f) about half as broad as long, with blunt end; setation as in *H. foliorum*, but apical setae supplemented by blunt spine; jointed proximoventral setae sparse.

PENIS (Fig. 7g). Very long, annulated throughout; pedicel broad, conspicuous; basidorsal protuberance (Fig. 7h) smaller than in *H. foliorum*.

Remarks. These morphological characteristics define sharply a species which occupies rock surfaces, wooden surfaces and the trunks and stems of the mangrove *Avicennia marina* in the upper intertidal of estuarine and sheltered waters, but does not inhabit the leaves of *A. marina*.

Distribution. Estuaries of New South Wales; Magnetic Island, north Qld.

The larval development of *H. popeiana*. As pointed out in the introduction, the larval development described by Egan & Anderson (1985) is that of *H. foliorum*. The present investigation has shown that the larvae of *H. popeiana* (Figs 8–12 and Tables 1–4) differ from those of *H. foliorum* in ways that allow each larval stage of the two species to be distinguished. There are also differences in the rate of larval development, compared under similar culture conditions at 20°C (Table 1 of this account and Table 1 of Egan & Anderson, 1985). Naupliar stages I–III develop at similar rates, but stages IV–VI proceed more slowly in *H. popeiana*. The cyprid stage is first reached in *H. foliorum* at 9 days, and in *H. popeiana* at 15 days.

The general dimensions of the naupliar stages and cyprid (Table 2) are similar in both species, as are many features of the dorsal shield, labrum and caudal papilla at each naupliar stage (Figs 8, 9). The differences between corresponding stages are set out in Table 3. Stages II–V (Fig. 8c,e,g,i) are more heavily spined in *H. foliorum*, while stage VI (Fig. 8k) is less spined. The cyprid of *H. foliorum* is also more sharply pointed at the anterior end in dorsal view than that of *H. popeiana* (Fig. 8m,n). There are no significant differences in the setal formulae of the naupliar limbs (Figs 10–12 and Table 4), but the naupliar plumose setae of *H. popeiana* have longer and more conspicuous setules than those of *H. foliorum*.

Functional morphology. CIRRAL ACTIVITIES. *Hexaminius popeiana* displays the full range of balanoid cirral activities described by Crisp &

Southward (1961) and redefined by Anderson & Southward (1987). On immersion, the animals briefly perform testing activity, accompanied by the release of bubbles of air from the mantle cavity. They then usually enter into pumping beat followed by normal beat, and variously alternate between these or between normal beat and fast beat. In any group of individuals, all of these levels of cirral activity can be observed, with some individuals showing withdrawal and closure of the operculum. Rocking of the closed operculum is a conspicuous activity. Prolonged cirral extension is rarely seen, and persists only for 1–2 seconds. Typical rates of cirral activity in *H. popeiana* are, pumping beat 5–6, normal beat 8–12 and fast beat 16–20 beats per 10s.

During normal beat and fast beat, the raised cirral fan achieves a less than vertical posture on each beat, always leaning slightly in a rostral direction. At the apex of cirral extension, the third maxillipeds are directed laterorostrally at the margins of the cirral fan.

Hexaminius foliorum, in contrast, is faster and more restricted in its range of cirral activities. Newly immersed animals release air bubbles in the usual way, but then enter directly into fast beat, with the operculum raised and open and the cirri fully exposed. Normal beat is rarely observed except as a brief preliminary to fast beat. Pumping beat and rocking of the closed operculum do not occur in this species. The rate of beating during fast beat is 18–23 per 10s and the cirral fan swings through a wide arc on each beat, leaning slightly carinally at the apex of the beat. The third maxillipeds remain more raised and rostrally directed than in *H. popeiana*, even at the apex of the beat.

COPULATORY ACTIVITIES. The difference in cirral activities between *H. popeiana* and *H. foliorum* is accompanied by a difference in the copulatory action of functional “males”. In general, the copulatory action in both species follows the typical mode for small estuarine balanoids, the penis being extended after cirral beating has commenced, and the cirri then being held extended while penis extension and probing occur.

In *H. popeiana*, when extension of the penis has been achieved, the extended rami of cirri IV–VI show a slight increase in curvature (Fig. 13) indicative of contraction of their retractor muscles. Functionally, this presumably increases the hydraulic pressure of the haemocoelic fluid in the extended penis. The extended maxillipeds also exhibit bouts of rapid muscular twitching coincident with the maxima of penis extension, perhaps further augmenting the enforcement of fluid into the penis.

In *H. foliorum*, copulatory activity is pursued very vigorously and it is usual to find several functional “males” simultaneously probing a functional “female”. In each “male”, when full penis extension is achieved, the distal ends of the rami of the long cirri curl up strongly (Fig. 14) and the extended

Table 1. Time taken at 20°C for the appearance of the larval stages in the most productive cultures of *H. popeiana* — No larvae detected. Blank space, time unknown.

Adult locality	Algal Food*	Time (No. of days) to appearance of naupliar stage						Cyprid
		I	II	III	IV	V	VI	
Folly Point	<i>P.l.</i> , <i>C.c.</i> , <i>S.c.</i>	1	1	2		10	11	15
Iron Cove	<i>P.l.</i> , <i>C.c.</i> , <i>S.c.</i>	1	1	2	3		9	—

**P.l.*, *Pavlova lutheri*; *C.c.*, *Chaetoceros calcitrans* (*Minutecellus polymorphus*); *S.c.*, *Skeletonema costatum*.

Table 2. Mean size of the cultured larval stages of *Hexaminius popeiana*

Stage	<i>n</i>	TL(mm)	SL(mm)	SP(mm)	W or D (mm)
I	5	0.22+0.01	—	—	0.12+0.01
II	14	0.33+0.002	—	—	0.15+0.004
III	12	0.40+0.02	—	—	0.17+0.01
IV	11	0.46+0.03	0.27+0.02	0.07+0.01	0.22+0.01
V	10	0.53+0.03	0.35+0.01	0.08+0.01	0.27+0.01
VI	5	0.62+0.03	0.44+0.02	0.09+0.01	0.33+0.01
Cyprid	1	0.47	—	—	0.23

n. Sample number; TL, total length; SL, shield length; SP, posterior shield spine length; W or D, shield width or cyprid depth. Confidence limits are 95%.

Table 3. Morphological differences between the naupliar stages of *H. popeiana* (this account) and *H. foliorum* (from Egan and Anderson 1985).

Stage	<i>H. popeiana</i>	<i>H. foliorum</i>
I	Anterior shield margin domed	Anterior shield margin convex
II	Anterior shield margin smooth. Lateral shield margin with fine spines.	Anterior shield margin spined. Lateral shield margin with coarse spines.
III	Lateral shield margin with few spines. Setae on median labral lobe serrate.	Lateral shield margin with many spines. Setae on median labral lobe simple.
IV	Frontolateral horns with large and small spines, not heavily ornamented. Setae on median labral lobe serrate.	Frontolateral horns with large spines, heavily ornamented. Setae on median labral lobe simple.
V	Frontolateral horns not heavily ornamented. One pair of long, slender dorsal shield spines, one short pair.	Frontolateral horns heavily ornamented. One pair of long, thick dorsal shield spines.
VI	Frontolateral horns heavily ornamented. One pair of long, slender dorsal shield spines, two short pairs. Posterior shield spines long (0.09+0.01 mm)	Frontolateral horns with short spines only. One pair of short dorsal shield spines. Posterior shield spines short (0.06+0.01 mm)

Table 4. Setal formulae for the nauplii of *Hexaminius popeiana*

Nauplius stage	Antennule	Antenna		Mandible	Endopodite
		Exopodite	Endopodite	Exopodite	
VI	<i>S:P:P:SPSP:SP:P:SP:S</i>	PPPP:8P	PPSP:SP:PD:SPPC:G	P:5P	SSSS:SSDD:SP ^D CP ^{sp} :PP ^D C:G
V	<i>S:P:P:SPSP:SP:S:P:S</i>	PPP:8P	PPSP:SP:PD:SP ^S PC:G	P:SP	SSSS:SSDD:SP ^D CP ^{sp} :PP ^D C:G
IV	<i>S:P:SPSP:SP:P:S</i>	PP:7P	PPSS:SP:PD:SPC:G	P:4P	SSSS:SDD:SP ^D S:PCP ^{sp} :PP ^D C:G
III	<i>S:SPSP:SP:P:S</i>	PP:5P	PPst ^S :SP:PD:SPC:G	P:3P:S	SSS:SP ^D S:PCP ^{sp} :PP ^D C:G
II	<i>SSPS:SP:P:S</i>	SP:4P:S	PPS:SP:PD:SPC:G	P:3P:S st	SSS:SP:SCP:PC:G
I	<i>SSSS:SS:S:S</i>	S:S:S:S	SSS:SS:SS:SS:G	S:S:S:S	SSS:SS:SS:SS:G

Setal types: S, simple; P, plumose; D, plumodenticulate; C, cuspidate; G, gnathobase; ^{sp}, spine; ^SP, simple, sometimes plumose; ^SP^S, plumose, sometimes simple; ^PD, plumose, sometimes plumodenticulate; st, setal stub; st^S, stub, sometimes short simple seta; Sst, simple seta, sometimes short simple seta, Pre-axial setae on the antennule are given in italics.

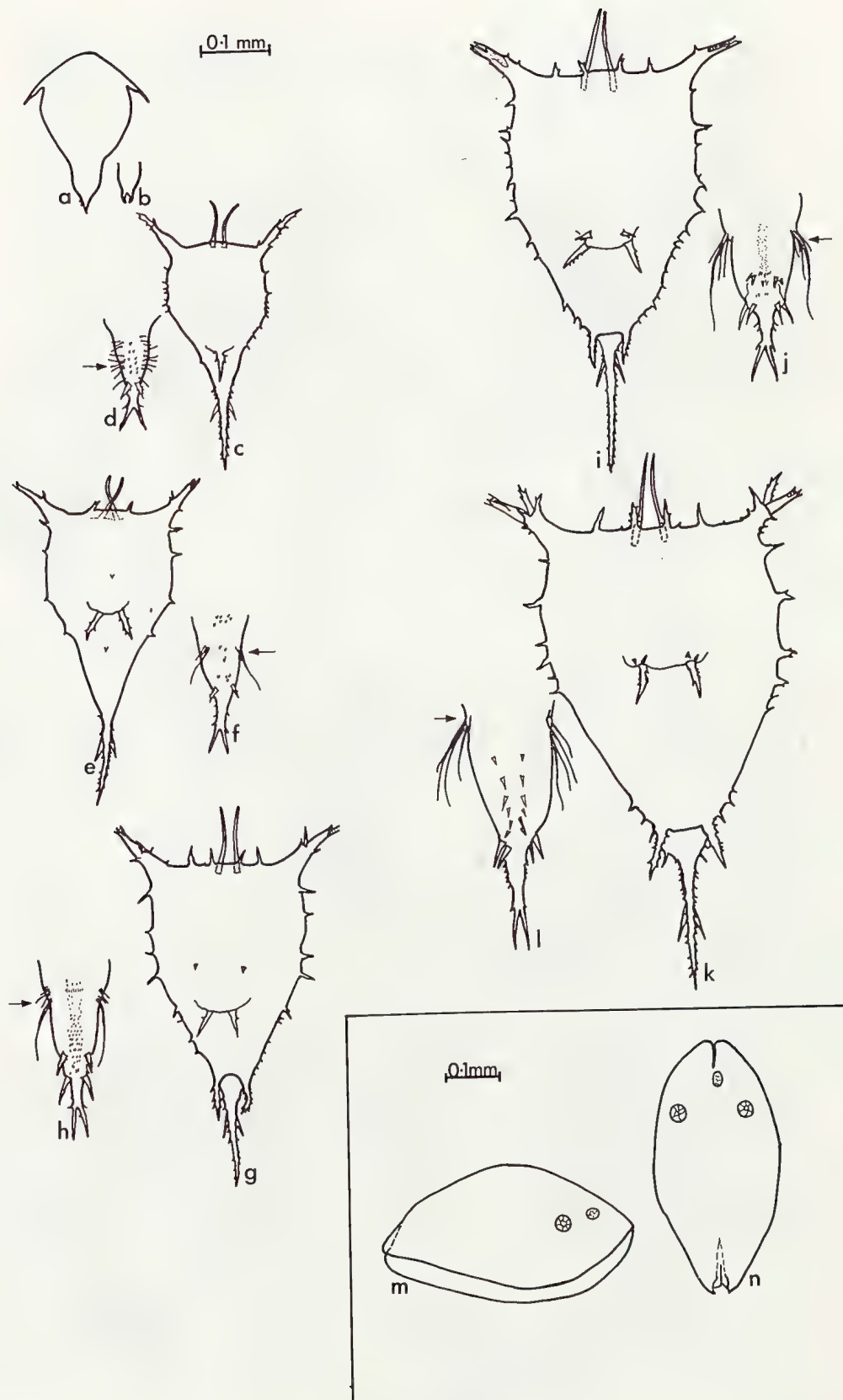


Fig. 8. *Hexaminus popeiana*. a, c, e, g, i, k, dorsal shield outlines of nauplius stages I-VI; b, d, f, h, j, l, ventral views of thoracoabdominal process of nauplius stages I-VI; m, cyprid in lateral view; n, cyprid in dorsal view. Arrows indicate the position of the maxilla for each nauplius stage. Scale 0.1 mm.



Fig.9. *Hexaminus popeiana*. a,b,d,f,h,j lateral view of thoracoabdominal process of naupliar stages I–VI; c,e,g,i,k labrum of naupliar stages I–VI, ventral (outer) surface. Arrows indicate the position of the maxilla for each naupliar stage. Scale 0.1 mm.

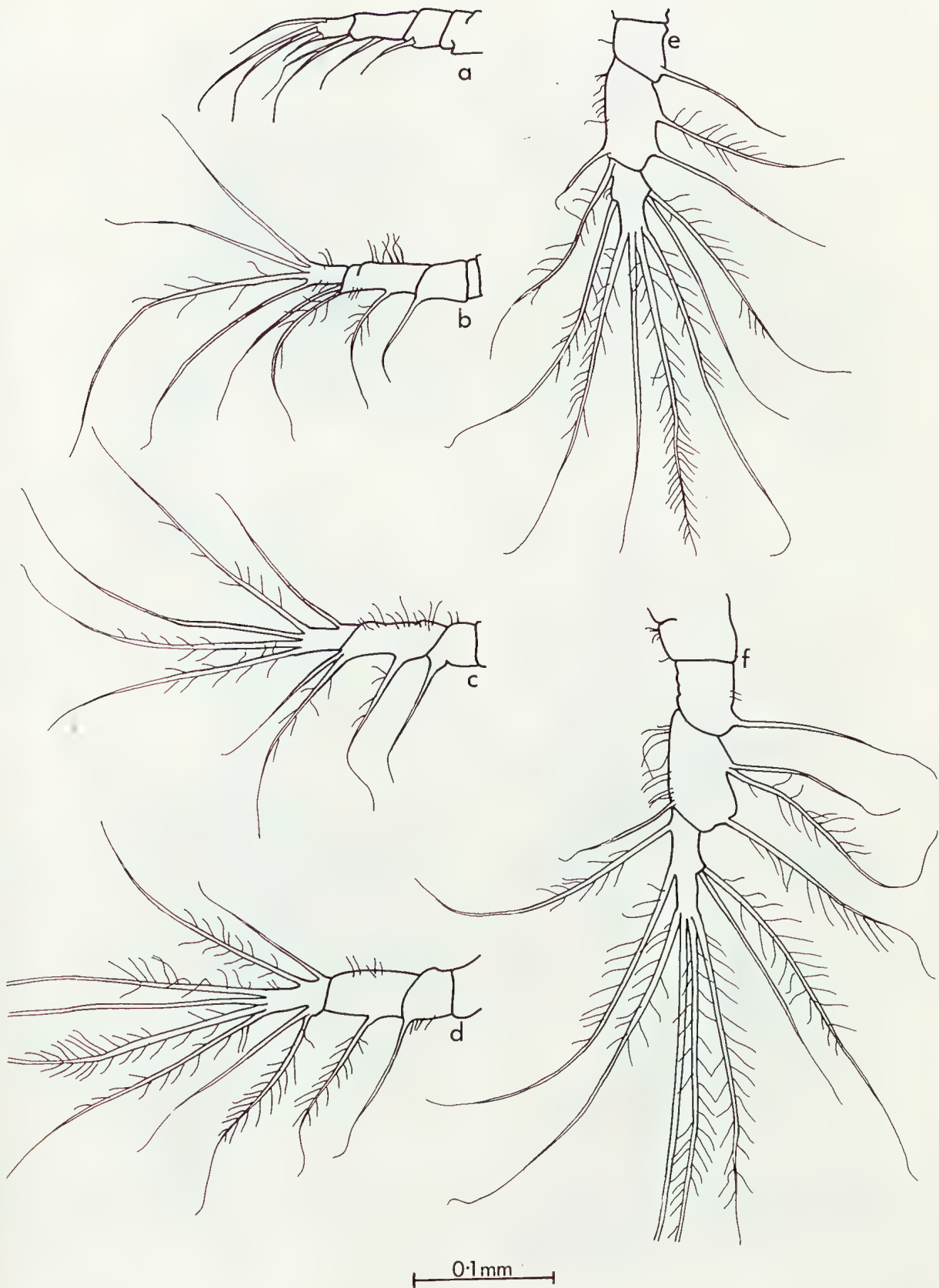


Fig.10. *Hexaminius popeiana*. a-f, antennule of naupliar stages I-VI. Scale 0.1 mm.



Fig.11. *Hexaminus popeiana*. a-f, antenna of naupliar stages I-VI. Scale 0.1 mm.



Fig.12. *Hexaminius popeiana*. a-f, mandible of naupliar stages I-VI. Scale 0.1 mm.

Fig.13. *Hexaminius popeiana*. "Male" posture during copulation.

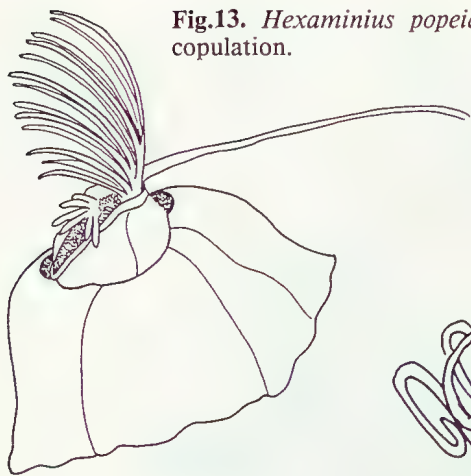


Fig.14. *Hexaminius foliorum*. "Male" posture (left) and "female" posture (right) during copulation.

maxillipeds beat together in continuous rapid motion, all indicative of the involvement of the whole body in a powerful copulatory effort. The copulatory intensity of *H. foliorum* is much higher than in *H. popeiana*. The recipient functional females also show a higher level of response, with gaping opercular valves and a partially extended, passive posture. The "females" of *H. popeiana*, in contrast, are more active and show a greater tendency to opercular closure in response to incipient probing.

Discussion

Balanomorphs on mangroves. The occupancy of mangrove surfaces by balanomorph barnacles is recorded for mangroves from most parts of their world range (Achituv, 1984), but barnacles have rarely been recorded on mangrove leaves. The usual surfaces to be encrusted are the trunks, stems, rhizophores and pneumatophores. Leaf occupancy has been noted only for *Euraphia withersi* in southern India (Daniel, 1972), some unspecified

chthamalids in South China (Wei & Lin, reported in Achituv, 1984) and *Elminius modestus* in northern New Zealand (Moore, 1944). All of these are species known to settle and grow on a variety of surfaces. We have also observed this phenomenon of settlement on different surfaces, including mangrove leaves, for *Balanus variegatus* and for *Elminius covertus* in New South Wales. The identification of *Hexaminius foliorum* as a species limited to the occupancy of mangrove leaves therefore appears to represent a unique level of restriction to this ephemeral habitat. It is made the more interesting by the sympatric existence of *Hexaminius popeiana*, whose larvae have access to but do not occupy the same leaves.

Functional morphology and reproduction of *H. foliorum*. The anatomical and functional differences between *H. foliorum* and *H. popeiana* are consistent with the view that *H. foliorum* is specialised as compared with *H. popeiana*. 1. The wall plates of *H. foliorum* are thinner and more fragile. 2. The basis of *H. foliorum* is thicker. 3. The tergoscute flaps of *H. foliorum* are more superficial and less deeply folded. 4. The opercular plates of *H. foliorum* are thinner,

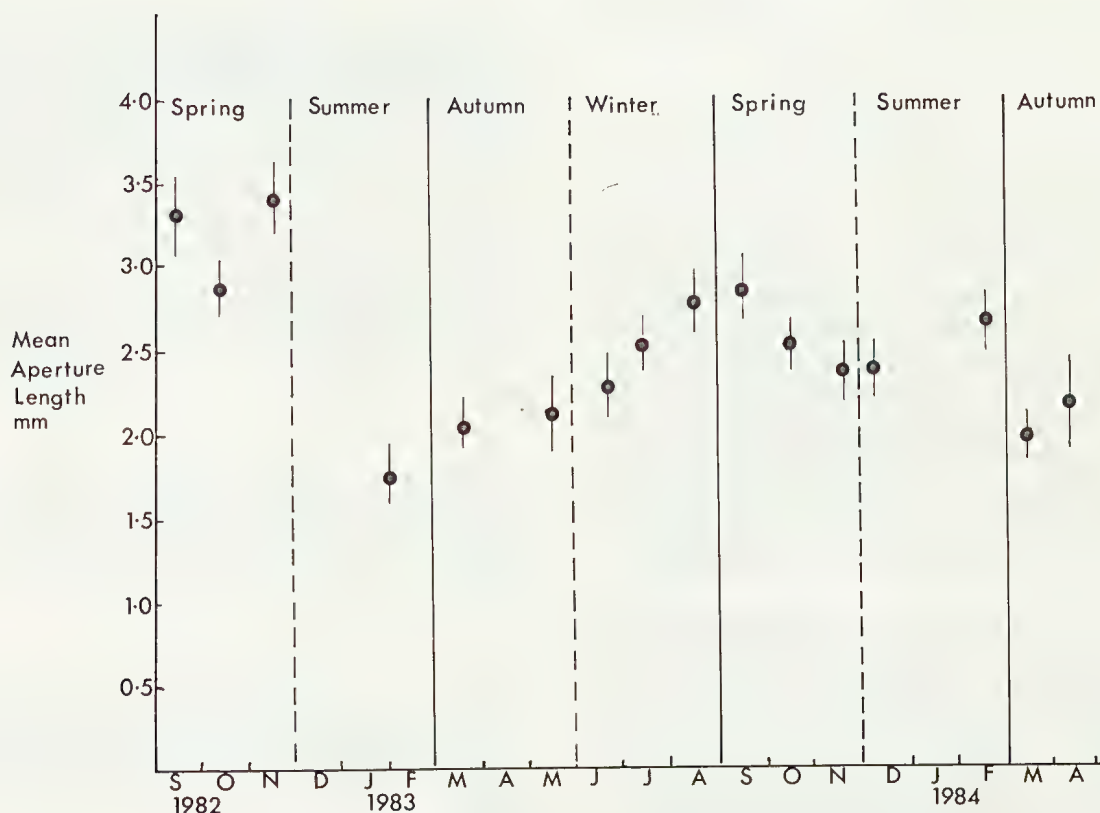


Fig.15. *Hexaminius foliorum*. Mean size of individuals in the population at Iron Cove, NSW, based on monthly samples of 50 individuals. Bars indicate standard error.

with weaker articulation of the scutum and tergum; the terga have fewer depressor muscle crests; the adductor muscle scar is less prominent on the scuta but the spur is longer on the terga. Opercular depressor muscles are also thinner. 5. The body of *H. foliorum* is longer and more streamlined, with thoracic limb bases more spread anteroposteriorly. 6. Cirrus I in *H. foliorum* has a shorter exopod and simplified setation; cirrus II has shorter rami; cirri IV–VI contrast in being longer and thinner, with more podomeres and longer setae. 7. Mandibles in *H. foliorum* are broader; maxillules narrower; maxillae are more prominent and setose. 8. The penis is shorter in *H. foliorum*, with reduced development of the pedicel.

Interpreting these differences in relation to habitat, the key factor may be that mangrove leaves are subject to leaf fall. Most of the leaf fall of *Avicennia marina* in the Sydney region occurs during the summer months (December–February), coincident with the major production of new leaves. There is an abrupt decrease in leaf fall during autumn (March–May) and little leaf fall during the winter months (June–August). An increase in leaf fall and leaf replacement occurs each spring (Goulter & Allaway, 1979).

Measurements of the mean size of individuals in

the population of *H. foliorum* at Iron Cove, NSW during 1983 and 1984 (Fig. 15) revealed a minimum mean size in late summer/early autumn, followed by a gradual increase in mean size during the autumn and winter months, commensurate with the relative stability of the substratum during that time. During the spring and summer, the high leaf fall and replacement was associated with fluctuations in mean size of *H. foliorum* as the population progressed once again to a minimum mean size. This is in accord with the loss of large adults due to leaf fall and the recruitment of young individuals onto new leaves. The life cycles of *H. foliorum* is thus an annual one, with population replacement mainly occurring each summer. At the same time, breeding and recruitment occur throughout the year (Egan & Anderson, 1985), with a reduction only in the autumn when the adult mortality resulting from the summer leaf fall is followed by a high incidence of immaturity in the succeeding generation. The continuous breeding of *H. foliorum* can be interpreted as an adaptation to maintenance of the species on a substratum that peaks in instability in the summer but is always ephemeral. *H. popeiana*, in contrast, inhabiting more stable and permanent substrata, shows a typical seasonal breeding pattern with a spring peak and little or no breeding during the

remainder of the year (Fig. 1). It seems likely that individuals of *H. popeiana* may live for more than one year, but this has yet to be tested.

In view of the similarities in body size, egg number and egg size in the two species, it is evident that *H. foliorum* releases more broods of larvae per individual per year and thus has a higher and more continuous reproductive effort than *H. popeiana*. The functional morphological modifications of *H. foliorum* are correlated with this reproductive difference. The thinner plates are indicative of more rapid growth. The longer, thinner captorial cirri with their longer setae imply a more rapidly acting cirral fan, achieving a faster feeding rate as a basis for faster growth and more sustained reproduction. The maxillipeds and mouthparts are modified in ways which suggest a more rapidly acting ingestive mechanism. The shorter penis, with reduced pedicel, may be correlated with a more rapid and intensive copulatory activity of *H. foliorum* as compared with *H. popeiana*.

Of these interpretations, two have been subjected to direct testing in the present investigation. The cirral mechanism is faster acting and more specialised in *H. foliorum* than in *H. popeiana*. The latter species displays the entire range of balanoid cirral activities, testing, pumping beat, normal beat and fast beat. *Hexaminius foliorum* displays only fast beat, which it performs more rapidly, with a greater sweep of the captorial cirri, than in *H. popeiana*. The copulatory mechanism in *H. foliorum* is also more specialised and more vigorous than in *H. popeiana*. Penis extension in functional "males" is frequent and rapid, and involves an intense effort in cirral curling and maxilliped beating. Functional "females" are passively receptive to probing by several males. In *H. popeiana*, these reproductive events are less intense and more leisurely in expression. The action of the species thus support the interpretation, based on morphology, that *H. foliorum* is specialised in ways that relate to the hazards of life on an ephemeral leaf habitat.

Larval development of *H. foliorum*. The morphological differences between the larvae of *H. foliorum* and *H. popeiana* are sufficient to support the separation of the two species, but do not offer any information on the relationship between them. Rates of larval development, however, are in accord with the concept that *H. foliorum* has higher rates generally than *H. popeiana* (nine days to cyprid as compared with 15).

Evolution of *H. foliorum*. We therefore conclude that *H. popeiana* is a six-plated elminiine as proposed by Foster (1982), but is confined to rocks, wood and mangrove trunks in the upper littoral of eastern Australian sheltered waters. Among mangroves of the central coast of New South Wales, another species, *H. foliorum*, occurs as an inhabitant of mangrove leaves, mainly occupying the underside of lower leaves subject to tidal immersion. The

functional morphology and reproductive biology of *H. foliorum* are specialised in ways related to the ephemerality of the leaf habitat. It seems likely that *H. popeiana* and *H. foliorum* have an ancestor-descendant relationship. Apart from the genetic questions raised by this interpretation, an ecological question is also presented. What are the settlement and recruitment patterns that lead the cyprids of *H. popeiana* to successful settlement on many surfaces, but not mangrove leaves, and *H. foliorum* to successful settlement on mangroves leaves only, thus resulting in populations of the two species that abut, but do not overlap, even on the same mangrove plant?

ACKNOWLEDGEMENTS. This project was supported by grants from the Australian Research Grants Scheme and the University of Sydney. Our special thanks to Dr S.W. Jeffrey, Division of Fisheries Research, CSIRO, who supplied the algal inocula, and to Dr J.K. Lowry for guidance in the ways of taxonomy.

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Two Species of Cavefishes from Northern Thailand in the Genera *Nemacheilus* and *Homaloptera* (Osteichthyes: Homalopteridae)

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ABSTRACT. Two new species of cavefishes from Mae Hong Son Province, northern Thailand represent the first record of cavefishes from that country. *Nemacheilus oedipus* n.sp. from Tham Nam Lang has degenerate eyes and is the first member of the Nemacheilinae with vestigial eyes and the seventh cavernicole. *Homaloptera thamicola* n.sp. from Tham Susa completely lacks eyes and is tentatively referred to *Homaloptera*, although it differs in details of mouth structure. It is the first blind cavernicolous representative of the Homalopterinae.

KOTTELAT, M. 1988. Two species of cavefishes from northern Thailand in the genera *Nemacheilus* and *Homaloptera* (Osteichthyes: Homalopteridae). Records of the Australian Museum 40(4): 225–231.

Cavefishes are known to occur in several areas of Asia, particularly in south-west Asia and in south China, areas which have extensive karstic formations. Although there are quite extensive karstic areas in Thailand, no cavefishes have been recorded from that country. In the last seven years I made several unsuccessful attempts to collect in a number of Thai caves. Despite this, I still think that some of the caves I visited without reward may have fishes. For example, the famous Chiang Dao caves, where I observed only shrimps (i.e., an unidentifiable juvenile of *Macrobrachium* which does not show any character that might indicate an adaptation to subterranean life; L.B. Holthuis, in litt.), are the subject of several tales involving cavefishes. According to inhabitants of Chiang Mai province, subterranean waters in Chiang Dao caves are inhabited by fishes which have numerous magical properties: they have no shadow and when they meet an obstacle, they can split, with each half going its own way and then fusing together once the obstacle is passed, etc. Unfortunately, I was unable to catch or see this very peculiar fish, if it exists, or any other cavefish in Thailand.

It was particularly pleasing when Dr. D. Hoese, of the Australian Museum, Sydney, sent me three specimens of two species of loaches which had

recently been collected in caves in Thailand. Although it is doubtful that the “magic” fish is among them, they are nevertheless of interest, one of them being the first known cave species of Homalopterinae and the other one being a new *Nemacheilus* with vestigial eyes.

Methods

The methods for making measurements and counts follow Kottelat (1984) except for the nomenclature of the cephalic lateral line system which is that of Illick (1956). When measurements are expressed as percent of head length, dorsal head length along the sagittal plane is meant. In anal and dorsal fin ray counts, $\frac{1}{2}$ refers to the last branched ray born by the same pterygiophore as the penultimate ray.

Measurements refer to standard lengths (SL) and head length (HL).

Nemacheilus oedipus n.sp.

Fig. 1

Type material. HOLOTYPE: AMS I.25986-002, 70.4 mm SL; Thailand: Mae Hong Son Prov.: Tham Nam Lang [= Nam Lang Cave], 19°31'N 98°09'E; J. Dunkley; 7 May

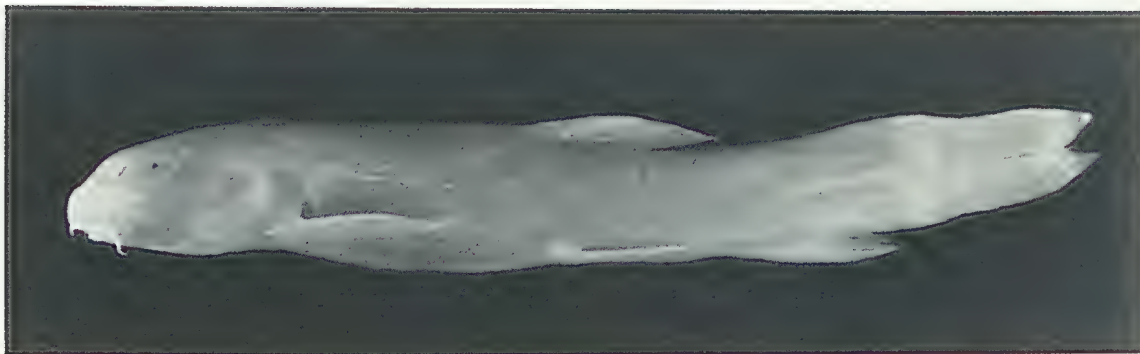


Fig.1. *Nemacheilus oedipus* n.sp. Holotype, AMS I 25986-002, 70.4 mm SL.

1985; PARATYPE: AMS I.25986-001, 1 ex., 74.3 mm SL; same data as holotype.

Diagnosis. The new species is distinguished from any known nemacheiline by the combination of the following characters: no colour pattern, and no externally visible eye but a pit in the center of the skin covering the orbit. See discussion below for differences from epigeian species occurring in same basin.

Description. Morphometric data in % of SL (data of holotype first, followed by those of paratype in brackets): total length 120.9 (122.5); lateral head length 24.6 (24.0); dorsal head length 22.3 (21.5); predorsal length 54.4 (54.4); prepelvic length 57.7 (58.1); pre-vent length 72.9 (75.1); preanal length 80.0 (80.9); head depth (at eye) 11.5 (11.2); head depth (at nape) 13.6 (13.3); body depth (at dorsal fin origin) 15.5 (13.2); depth of caudal peduncle 11.5 (9.4); length of caudal peduncle 13.5 (13.6); length of dorsal crest on caudal peduncle 16.8 (14.9); length of ventral crest of caudal peduncle 10.2 (8.3); snout length 12.2 (11.2); head width at nares 10.8 (11.0); maximum head width 16.8 (16.8); body width at dorsal fin origin 11.1 (10.1); body width at anal fin origin 6.4 (5.9); width of bony interorbital 5.7 (5.8); width of mouth gape 6.7 (7.1); height of dorsal fin 15.9 (15.1); height of anal fin 17.0 (16.6); length of pectoral fin 19.3 (19.1); length of pelvic fin 17.2 (16.7); length of upper caudal lobe 23.0 (21.5); length of lower caudal lobe 21.6 (20.6); length of middle caudal rays 17.9 (13.9).

Elongate species of nemacheiline with compressed body, blunt snout. Pectoral fin (12 rays) reaching slightly beyond halfway to pelvic fin base. Axillary pelvic lobe present. Pelvic fin (8 rays) origin below 2nd to 3rd branched dorsal ray, not reaching vent which is situated some distance in front of anal fin. Anal fin (3/5½ rays) not reaching base of caudal fin. Caudal fin (9+8 branched rays) forked. Caudal peduncle 1.17 (1.44) times longer than deep, with dorsal and ventral crest present, in part sustained by rudimentary rays. Dorsal fin (4/8½ rays) with straight or slightly concave distal margin.

Body entirely covered by embedded scales, each

circular in form with a wide (about half of scale diameter) focus. Scales are slightly more sparsely set in front of dorsal fin. Scales immediately above and below lateral line not conspicuously larger than those of adjacent rows. Complete lateral line, with about 100 (87) pores which are difficult to count with precision. Cephalic lateral line system with 7 (6) supraorbital, 3+13 infraorbital, 12 (11) preoperculo-mandibular and 3 supratemporal pores. No externally visible eye but pit in center of the skin covering orbit (Fig. 2); vestigial remains of eye deep under skin clearly distinct as small black area. Anterior nostril pierced at base of front side of triangular flap which, when folded back, completely covers posterior nostril (Fig. 3c).

Mouth arched, its gape about 2½-3 times wider than long (Fig. 3a). Upper jaw with well-developed processus dentiformis. Lower jaw with shallow median depression. Lips thin, nearly smooth, upper one with very slight median incision, lower one with median interruption. Maxillary barbels reaching somewhat beyond vertical of eye pit. Outer rostral barbels reaching slightly beyond base of maxillary barbel; inner rostral barbels not reaching corner of mouth. Intestine with bend immediately behind stomach (Fig. 3b). Stomach of paratype (a male) nearly empty, its content not identifiable. Air bladder without free posterior chamber.

No unculi or tubercles. No known sexual dimorphism, but in 2 specimens, the second pectoral ray is thickened. This is known to be secondary male sexual feature in several other nemacheilines.

Colouration. Body and fins whitish.

Distribution and habitat. Only known from the type locality, Tham Nam Lang, Mae Hong Son Province, Thailand. Tham Nam Lang is an outflow cave east of Nam Khong, a tributary of Nam Mae Pai, itself a tributary of Salween River. The stream flowing out of Tham Nam Lang is probably part of Nam Lang which sinks at about 19°32'N 98°13'E. Nam Lang is one of several streams now flowing in karstic endoreic basins which formerly constituted a single drainage tributary of Nam Khong (as judged from topographic information on 1:250,000 maps of



Fig.2. *Nemacheilus oedipus* n.sp. Holotype, AMS I 25986-002, 70.4 mm SL. Note black ocular pit.

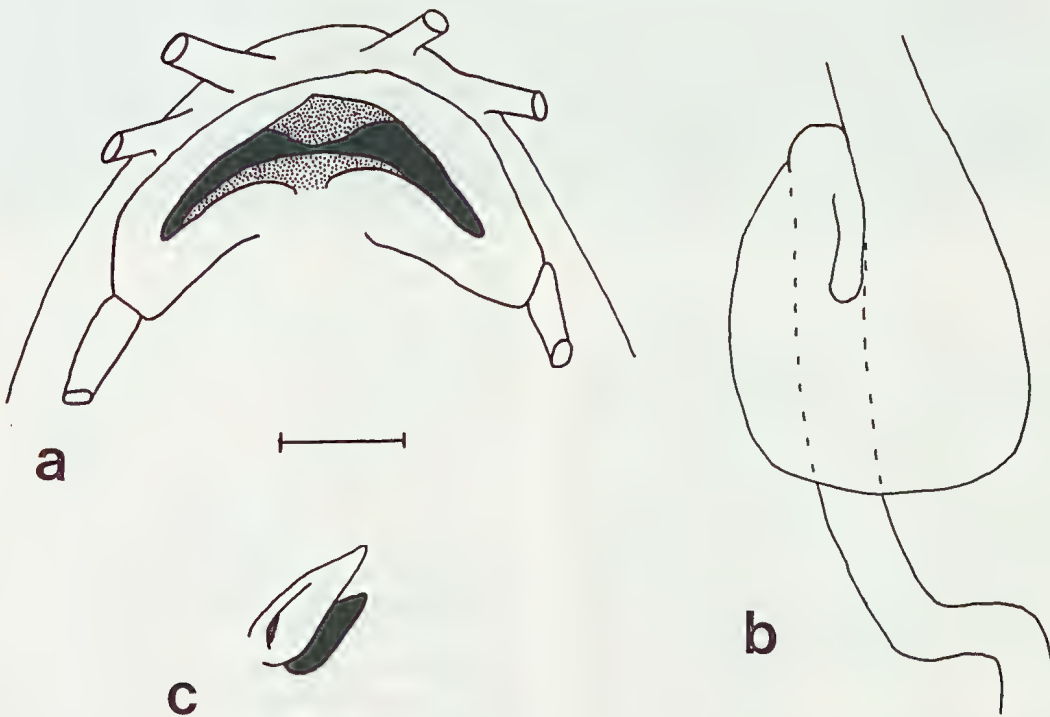


Fig.3. *Nemacheilus oedipus* n.sp. Paratype, AMS I 25986-001, 74.3 mm SL. a: mouth, b: digestive tract, c: left nostril. Scale bar: 2 mm.

the Thai map series 1501 S). The fishes were collected in a pool of moving water about 1 km inside the entrance.

Etymology. Oedipus, a mythic Theban king who tore out his eyes (see classical tragedies by Aeschylus, Sophocles, Euripides, Seneca and Corneille). Treated as a name in apposition.

Discussion. Several species of nemacheilines have already been reported from caves. Some have normal eyes and colour pattern, e.g. *Nemacheilus fasciatus* (Valenciennes, 1846) from cave Guva Gremeng in Java (Weber & de Beaufort, 1916; Kottelat, 1984). Others are colourless with normal eyes, e.g. *N. evezardi* Day, 1878 from an unspecified cave in India (Greenwood, 1978), and a species from Siju Cave in Meghalaya, India, identified as *Nemacheilus* sp. by Hora (1924), *N. beavani* Günther, 1868 by Hora (1935) or *N. multifasciatus* Day, 1878 by Pillai & Yazdani (1977). Others are white and eyeless, such as *N. smithi* Greenwood, 1976 from Iran, *N. gejiuensis* Chu & Chen, 1979 from Yunnan Province of China, *N. starostini* Parin, 1983 from Turkmenia, *N. xiangxiensis* Yang, Yuan & Liao, 1986 from Xiangxi, Hunan Province, China, and *N. anophthalmus* (Zheng, in Guangxi Fisheries Research Institute etc., 1981) from Guangxi Province, China (Zhao, 1983). *Nemacheilus oedipus* is the first species with vestigial eyes.

None of these cavernicolous species are apparently closely related. Their respective habitats are very distant from each other. Nemacheilines are benthic fishes usually hiding under stones; this habitat preference certainly favoured their entering subterranean waters. This almost certainly occurred independently in the various cave systems and relationships must be looked for with epigeal species. The subfamily Nemacheilinae includes some 430 nominal species, about 260 of them are considered valid (Kottelat, ms). Their systematics is still chaotic both at specific and supraspecific level. A few genera only are actually diagnosed by sets of synapomorphies and all remaining species are placed in the catch-all genus *Nemacheilus* Bleeker, 1863. *Nemacheilus oedipus* belongs to this last category. Its relationships will probably remain unclear as long as those of epigeal species are unresolved. As *N. oedipus* is possibly derived from one of the epigeal species presently in the Nam Mae Pai basin (to which Tham Nam Lang belongs), it is worth comparing it with them. However, one must remember that organisms living in caves may also be relicts of a former fauna. The following nemacheilines have already been reported from Nam Mae Pai basin: *Acanthocobitis zonalternans* (Blyth, 1860), *Neonoemacheilus labeosus* (Kottelat, 1982), *Nemacheilus poculi* Smith, 1945, *N. reidi* Smith, 1945 and two undescribed species (Kottelat, ms).

Acanthocobitis zonalternans is distinguished by strongly papillated lips, a rounded caudal fin, more

branched dorsal rays (9–11½ vs 8½) and less branched caudal rays (8+7–8 vs 9+8). The largest recorded *A. zonalternans* is 44 mm SL, while the two *N. oedipus* are 70.4–74.3 mm SL, and the males of *A. zonalternans* have a suborbital hook (an external process of lateral ethmoid), a feature not present in the paratype of *N. oedipus* which is a male. *Neonoemacheilus labeosus* has hypertrophied lips forming a preoral cavity (Kottelat, 1982; Zhu & Guo, 1985) and the presence of a suborbital hook in males. *Nemacheilus poculi* has less branched caudal rays (8+7 vs 9+8). The two undescribed species have a suborbital hook in males, a smaller size, and one has a differently shaped upper jaw and an emarginate caudal fin.

Nemacheilus reidi is one of the most widely distributed nemacheilines in the Nam Mae Pai and Mae Nam Yuam basins (Salween drainage) in northern Thailand; it reaches at least 89 mm SL and, if the ancestor of *N. oedipus* is still living in the Nam Mae Pai basin, *N. reidi* could be a likely candidate. Beside absence of colour pattern, possession of degenerate eyes, the new species is distinguished from *N. reidi* by its forked caudal fin (vs emarginate) and by the following morphometric characters: greater dorsal head length (21.5 & 22.3 vs 18.6–21.3% SL), smaller lateral head length (110 & 111 vs 116–126% HL), greater prepelvic length (57.7 & 58.1 vs 49.6–53.3% SL), greater pre-vent length (72.8 & 75.1 vs 66.1–71.0% SL), greater preanal length (80.0 & 80.9 vs 72.6–78.7% SL), slenderer body (depth at dorsal fin origin 13.2 & 15.5 vs 15.9–20.9% SL; 61 & 69 vs 80–112% HL), slenderer caudal peduncle (depth 9.4 & 11.5 vs 12.7–14.2% SL; 44 & 52 vs 64–76% HL; length 13.5 & 13.6 vs 13.4–17.9% SL; 61 & 63 vs 67–96% HL), thinner body (10.1 & 11.1 vs 12.2–14.9% SL at dorsal fin origin; 5.9 & 6.4 vs 7.8–9.9% SL at anal fin origin); smaller bony interorbital width (5.7 & 5.8 vs 5.8–7.3% SL; 26 & 27 vs 31–36% HL) [morphometric data for *N. reidi* were obtained from 18 specimens 40.8–71.3 mm SL]. Some of these differences (widths and depths) are possibly related with the reduced food availability in the cave environment.

Homaloptera thamicola n.sp.

Fig. 4

Type material. HOLOTYPE: AMS I.25987-001, 28.4 mm SL; Thailand: Mae Hong Son Province: Tham Susa [= Susa Cave], 19°28'N 98°08'E; J. Taylor, 7 May 1985.

Diagnosis. The new species is immediately distinguished from any other species of *Homaloptera* by the following unique characters: absence of eyes; body naked, colourless; pectoral fin with 22–23 rays (vs 20 or less), 15–16 of them being branched (vs 13 or less), 10 branched pelvic rays (vs 9 or less) and two barbels at each corner of mouth.

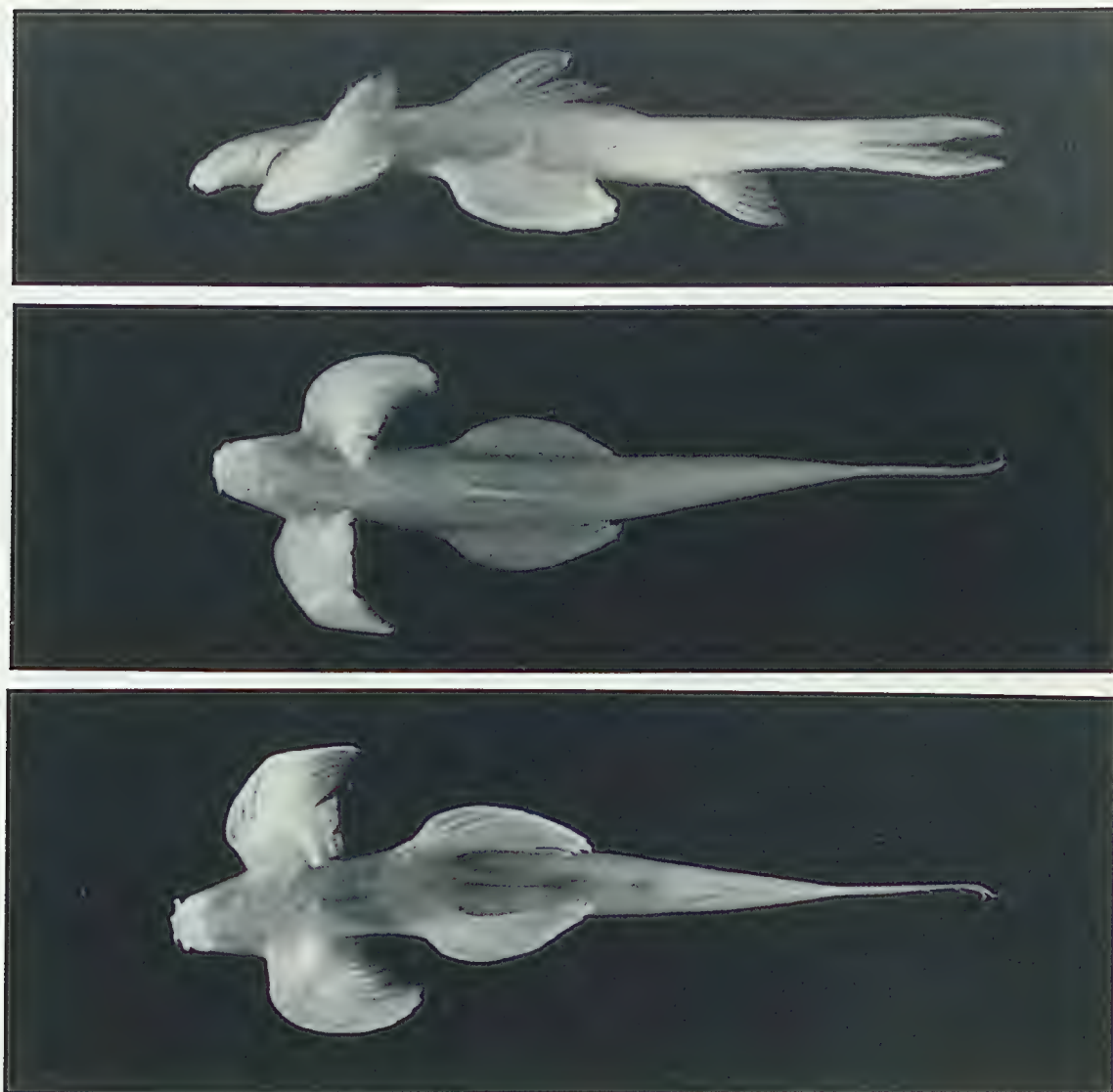


Fig.4. *Homaloptera thamicola* n.sp. Holotype, AMS I 25987-001, 28.4 mm SL.

Description. Morphometric data (in % of SL): total length 130.3; lateral head length 16.5; dorsal head length 19.7; predorsal length 43.3; prepelvic length 39.1; pre-vent length 74.3; preanal length 79.2; head depth (at nape) 8.1; body depth (at dorsal fin origin) 10.9; depth of caudal peduncle 7.4; length of caudal peduncle 20.1; head width at nares 9.9; maximum head width 13.0; body width at dorsal fin origin 13.7; distance between posterior extremity of pelvic fin bases 7.7; height of dorsal fin 19.4; height of anal fin 18.7; length of pectoral fin 28.5; length of pelvic fin 29.9; length of upper caudal lobe 26.8; length of lower caudal lobe 27.8; length of middle caudal rays 15.1.

Elongated homalopterine, with short, blunt head; nearly terete trunk, large fins. Gill opening extending to ventral surface in front of pectoral fin base. Pectoral fin (7 simple, 15–16 branched rays) reaching to base of pelvic fin with its length much greater than

body width. No axillary pelvic flap. Pelvic fin (2 simple, 10 branched rays) origin below dorsal fin origin, not reaching vent which is somewhat in front of anal fin. Anal fin ($3/5\frac{1}{2}$ rays) falcate. Caudal fin ($9+8$ branched rays) deeply forked with subequal lobes. Caudal peduncle 2.71 times longer than deep. Dorsal fin ($4/9\frac{1}{2}$) with straight distal margin. Unculi forming adhesive pads on inferior surface of 7 anterior pectoral rays and 3 anterior pelvic rays.

Body naked; skin smooth, without tubercles or unculi. About 32 myomeres. Lateral line complete with about 70 pores. Cephalic lateral line system apparently consisting only of infraorbital canal, without pores. No eye.

Mouth arched. Both jaws exposed. Anterior lip thin and smooth. Preoral and rostral groove present. Posterior lip inconspicuous, smooth, not continuous with anterior lip, with deep postoral groove and no postlabial groove. Four short rostral barbels situated

anteriorly on snout, not forming stiff lobes between them. Two barbels at each corner of mouth: small one continuous with lower lip, longer one originating from below anterior lip (Fig. 5).

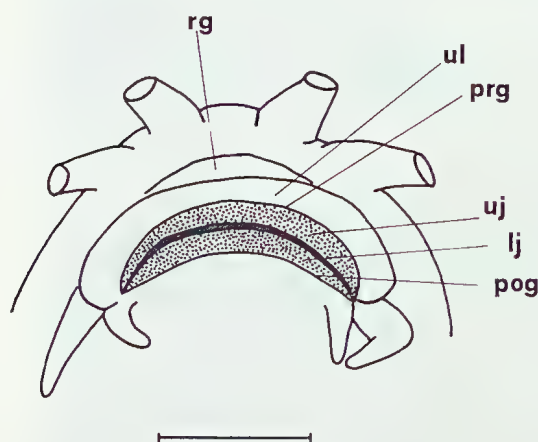


Fig. 5. *Homaloptera thamicola* n.sp. Holotype, AMS I 25987-001, 28.4 mm SL. Mouth. rg: rostral groove, ul: upper lip, prg: preoral groove, uj: upper jaw, lj: lower jaw, pog: postoral groove. Scale bar: 1 mm.

Colouration. Body and fins whitish; unculiferous pads under pelvic and pectoral rays orange brown.

Distribution and habitat. Only known from the type locality, Tham Susa, in Mae Hong Son Province, Thailand. Tham Susa is an outflow stream cave rising to the east of Nam Khong, a tributary of Nam Mae Pai, itself a tributary of the Salween River. The holotype was found on a ledge apparently climbing up a small waterfall about 0.6 km from the cave entrance.

Etymology. Based on *tham*, latin transcription of the Thai word for cave; *cola*, from the latin *colere*, meaning to inhabit.

Discussion. Relations among and within homalopterine 'genera' are presently poorly understood. In addition to characters which obviously are adaptations to the cave environment (lack of eyes, pigmentation and scales), the new species exhibits some unique characters as listed in the above diagnosis and in the organisation of lips and barbels. I find them to be close to the range of variation in *Homaloptera* and thus suggest that this is the approximate position of the species. The mouth organisation is somewhat peculiar, especially the two barbels at each corner. The lower lip structure is similar in several species (e.g. *H. gymnogaster* Bleeker, 1853, *H. sexmaculata* Fowler, 1934 and a species from Thailand tentatively identified as *H. zollingeri* Bleeker, 1853). *Homaloptera* as presently understood seems to be a somewhat unnatural assemblage consisting of three distinguishable units possibly worth consideration at the generic level. I

am investigating this problem and once it is solved, a more appropriate statement of the relationships of the new species might be possible.

Neohomaloptera Herre, 1944 is distinguished from *Homaloptera* nearly only by the possession of two maxillary barbels. I agree with Alfred (1969) that its type and only included species *N. johorensis* Herre, 1944 is better considered as a member of *Homaloptera*. I demonstrated that in another homalopterine lineage (*Balitora* and related genera; Kottelat & Chu, 1988a) the second maxillary barbel is merely an elongate papilla. Most keys to genera of Homalopteridae (Smith, 1945; Silas, 1954; Chen, 1978) are based on Hora (1932) and are incorrect in at least one important character: all consider that in *Homaloptera* the rostral groove is absent or poorly developed. In all species of *Homaloptera* (about 15) that I have examined, the rostral groove is well developed and conspicuous. Following Hora's classification, Smith (1945) described a new *Homaloptera* as a new genus, *Balitoropsis*; *Balitoropsis yunnanensis* Chen, 1978 also is a *Homaloptera* s.l. (Kottelat & Chu, 1988b).

Inclusion of *Homaloptera thamicola* in any other genus is not possible as all others have a more complicated mouth structure. Also known from this area are *Balitora* (Kottelat, 1988) and *Hemimyzon* (Kottelat, unpublished); they belong to a distinct lineage characterised by lips with numerous well-developed papillae and rostral barbels inserted below the snout and forming between them stiff lobes. In addition, *Hemimyzon* has three or more simple pelvic rays (Kottelat & Chu, 1988b).

This is the first record of either a subterranean or blind member of the subfamily Homalopterinae.

Formerly, the absence of eyes, scales and pigment would have been sufficient to consider the new species as belonging to a distinct genus. However, I agree with Roberts & Stewart (1976) that too much importance has been attributed to such characters and that, in the absence of more significant characters, specific distinction only is warranted.

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Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales

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ABSTRACT. Minute mollusc fauna of Late Tournaisian age from thin limestone bands of the upper part of the Dangarfield Formation near Gundy, Upper Hunter, New South Wales are classified and described. Eighteen species among 38 gastropod species referable to 31 genera are described as new — *Onychochilus minutissimus*, *Peruvispira gundyensis*, *Glabrocingulum obesum*, *Hesperiella robertsi*, *Borestus costatus*, *Araeonema microspirulata*, *Microdoma angulata*, *Eucochlis australis*, *Naticopsis* (*Naticopsis*) *osbornei*, *Aclisina turgida*, *Stegocoelia* (*Stegocoelia*) *nodosa*, *Stegocoelia* (*Hypergonia*) *elongata*, *Stegocoelia* (*H.*) *tenuis*, *Loxonema elegantissima*, *Hemizyga* (*Hemizyga*) *decussata*, *Cyclozyga sinusigera*, *Soleniscus callosus* and *Donaldina filosa*. Twenty European and North American generic names are introduced for the first time to the Australian gastropod fauna.

Two new scaphopod genera, *Scissuradentalium* and *Pipadentalium*, and four new species, *Fissuradentalium longistriatum*, *Scissuradentalium runnegari*, *Plagioglypta numerosa* and *Pipadentalium protruberans*, are proposed. One species of hyolitha, *Hyolithes minutissimus*, is described. Nine bivalve forms including two unknown taxa are illustrated, but not described here. All mollusc specimens are chloritised.

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Rich marine fossil faunas consisting of assemblages of brachiopods, gastropods, bivalves, crinoids, corals, fenestellid bryozoa, cephalopods and trilobites, are present in the calcareous mudstone and the bioclastic limestone of the upper part of the Dangarfield Formation. Microfossil faunas comprising gastropods, bivalves, scaphopods, hyoliths, ostracods, hexactinellid sponge spicules, conodonts and fish teeth were recovered from the bioclastic limestone by using standard acetic acid techniques. In this paper, a well-preserved minute molluscan fauna totalling approximately 2,000 specimens are classified.

Carboniferous molluscs have been known in New South Wales since the work of Etheridge (1890a,b, 1896, 1898, 1907) on fauna from the Port Stephens, Paterson, and Babbinoon Districts. Occasional descriptions of molluscs (de Koninck, 1898; Dun & Benson, 1920) and faunal lists (Benson, 1921) have appeared. Additional new species of molluscs have been described from Old Cannindah, Qld (Maxwell, 1961), from near Sherwood, west northwest of Kempsey (Campbell, 1961, 1962), from the Werrie and Belvue Synclines (Campbell & Engel, 1963) and from near Barrington (Campbell & McKelvey, 1971).

Materials and Methods

Each limestone sample weighing about 20 kg was acidised by using standard acetic acid techniques as applied for conodont preparation.

The residues were hand sorted beneath a low power binocular microscope. Illustrations were obtained using scanning electron microscope, JEOL JSM-U3.

All type specimens are given Australian Museum registration numbers unless stated otherwise, and are housed in the Australian Museum, Sydney.

Abbreviations used at the higher taxonomic levels are as follows: C.—Class, S.C.—Subclass, O.—Order, S.O.—Suborder, S.F.—Superfamily, T.—Tribe.

Type Locality

Bioclastic limestone lenses of the Dangarfield Formation; 70 m west to the junction of the Scone-Gundy road and the entrance to 'Marohn' homestead, 2.6 km southwest of Gundy, NSW. All localities mentioned in systematics (A-1, A-3, A-4, C-32, C-34 and C-36) are located within the extension of the limestone lenses as shown in Map 1.

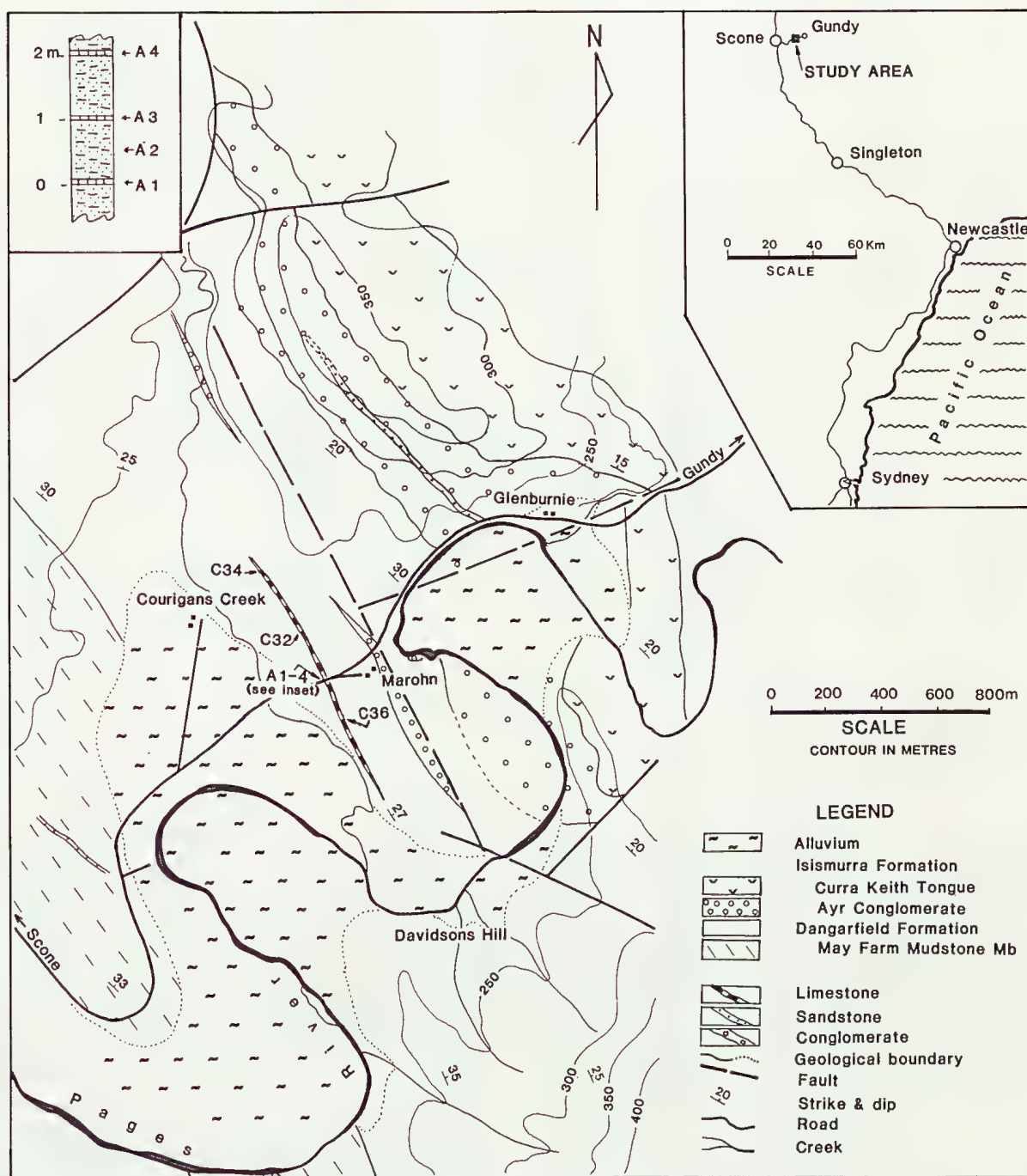
Stratigraphy

DANGARFIELD FORMATION. The Dangarfield Formation was originally defined by Oversby & Roberts (1973) as the thick sequence of mudstone and subordinate lithic sandstone and oolitic and crinoidal limestones overlying the tuffs and

tuffaceous sandstones of the Kingsfield Beds. The lowermost part of the formation which consists of lithic sandstones and siltstones grading into calcareous skeletal mudstones and wackestones was separated by Mory (1978) as a new formation and named the Macqueen Formation. He further divided the lower part of the Dangarfield Formation into two members: the Wroxley Lithic Sandstone Member and Brushy Hill Limestone Member. The name Brushy Hill Limestone was first used for the oolitic limestone sequence by Osborne (1928, 1950) in referring to sedimentary rocks now known as the Dangarfield Formation and volcanic rocks now known to belong to the Isismurra Formation. The succeeding sequence of the Dangarfield Formation is subdivided into two units, on the basis of lithology, and the lower part is named the May Farm Mudstone Member. The upper part is undivided and retained as Dangarfield Formation. The geology and stratigraphy of the study area are shown in Map 1 and Section 1.

MAY FARM MUDSTONE MEMBER. The May Farm Mudstone Member consists largely of monotonous brown and grey mudstones with minor lithic sandstone and limestone. It is delineated by the top of the underlying Brushy Hill Limestone Member and by the base of the lowest medium to coarse calcareous lithic sandstone cropping out along the western foot of the MacIntyres Mountain. This member was initially named by Mory (1975) after 'May Farm' homestead which lies near the northern foreshores of Lake Glenbawn, east of Brushy Hill. At the base of the member, the mudstone contains ooids gradually decreasing upwards and abundant allochthonous solitary rugose corals, as well as common brachiopods and crinoid stems. A 1.5 m thick fine grained calcareous sandstone outcropping along the strike direction through 'May Farm' homestead appears to be unfossiliferous. The thickness of the member is approximately 480 m.

UPPER PART OF THE DANGARFIELD FORMATION. The base of the unit is gradational and taken at the base of the lowest lithic/calcareous sandstone overlying conformably the May Farm Mudstone Member. The upper limit is the base of the Ayr Conglomerate Member of the Isismurra Formation. The unit consists of a thick sequence of greenish-grey to brownish-grey sandy mudstone, calcareous to lithic sandstone, conglomerate, and bioclastic limestone lenses. This unit outcrops on the western slope of the MacIntyres Mountain where the thickness ranges from 510 to 540 m. The lithofacies to the north of Pages River are noticeably different from that to the south of the river. About 70 m west of the entrance to 'Marohn' homestead, three bands of grey bioclastic limestone interbedded in mudstone, crop out at the roadside connecting Scone and Gundy (Map 1). Each limestone band ranges in thickness from 0.1 to 0.2 m and the limestones can be traced 800 m in northwest-southeast direction. The



Map 1. Geology and location map of the study area.

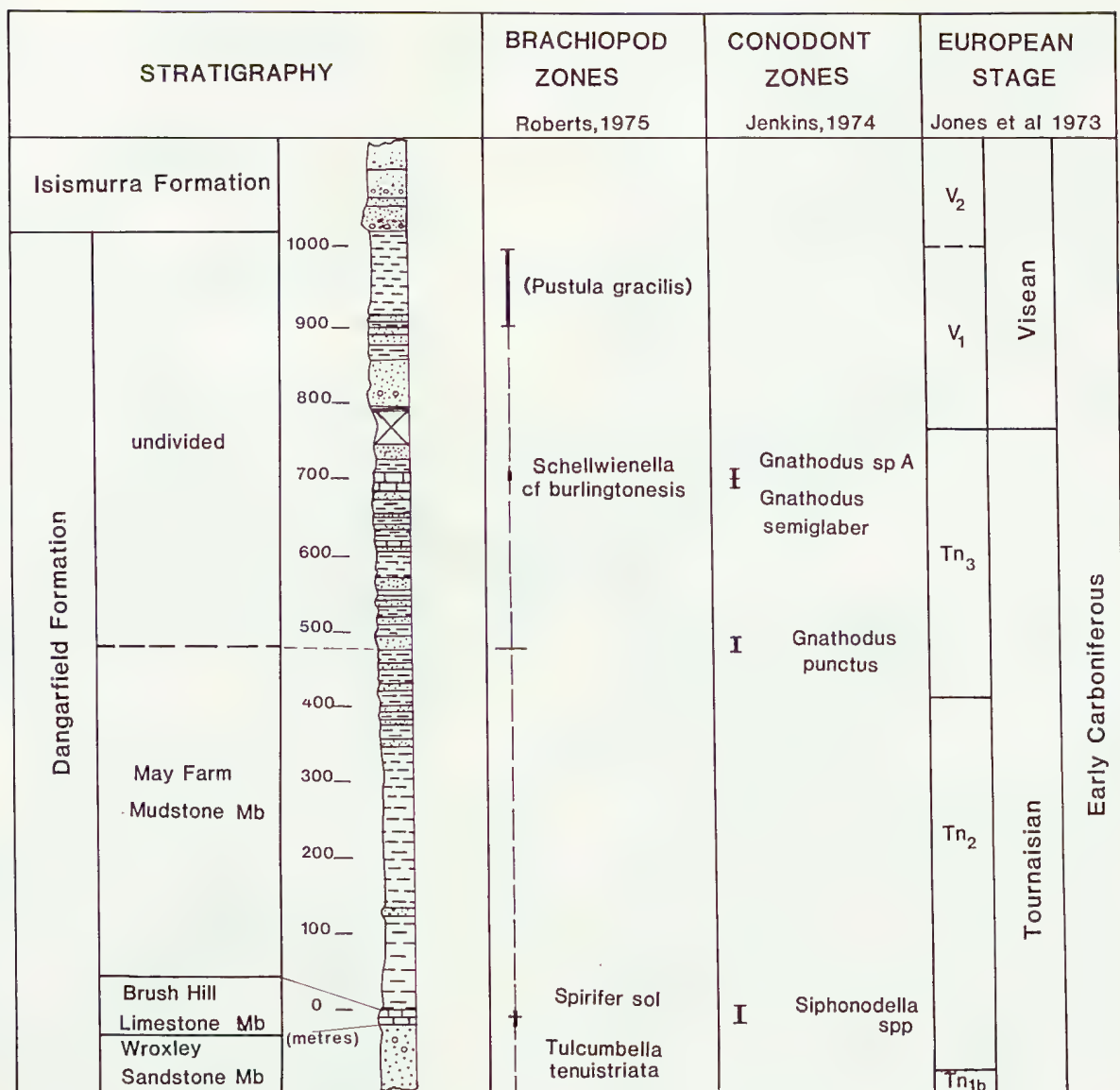
upper part of the formation, on the upper hill of the MacIntyres Mountain consists of a greenish-grey sandy mudstone containing abundant fenestellid bryozoa as well as brachiopods, macro-gastropods and crinoid stems.

Geological Age of Fossil Assemblage

EVIDENCE FROM OTHER LOCAL FAUNA. Research on Early Carboniferous brachiopods and conodonts

has been extensively carried out in the study area (Roberts & Oversby, 1974; Jenkins, 1974; Roberts, 1975).

Four conodont zones were proposed by Jenkins (1974) in the Dangarfield Formation, and were correlated with sequences from North America and Belgium. The bioclastic limestone of the Dangarfield Formation on the Scone-Gundy road near 'Marohn' homestead lies within conodont *Gnathodus* sp. A zone. This zone, on comparison with the Belgian



Section 1. Stratigraphy of the study area and faunal zones (graphic section between Brush Hill and 'Glenburnie', modified from Roberts & Oversby, 1974).

stratotypes, correlates with Tn_{3a} or, more probably, Tn_{3b} (the late, not latest, Tournaisian) (Jenkins, 1974).

Three brachiopod zones were identified in the Dangarfield Formation (Section 1). The bioclastic limestone lenses lie also within the brachiopod *Schellwienella* cf *burlingtonensis* zone which is widespread throughout the Rouchel district (Roberts & Oversby, 1974). Ammonoid data in this area of Germany suggest that *S. cf burlingtonensis* zone is Cu_{11a} in age (Jones et al., 1973) which is consistent with the age indicated by the conodonts.

EVIDENCE FROM GASTROPOD FAUNA. Thirty-four genera and subgenera of gastropods recognised in this study were originally named in Europe or North America and most of them are known to occur in

both continents. However *Scalitina*, *Hesperiella*, *Turbonitella* and *Palaeozygopleura* have not yet been recorded in North America, while *Rhabdotocochlis*, *Eucochlis*, *Hemizyga* and *Cyclozyga* have not yet been recorded in Europe.

The gastropod genera found in the present study area have various ranges within the Palaeozoic and only *Naticopsis* persists into the Mesozoic. Two genera, *Aclisina* and *Turbonitella*, and one subgenus, *Angyomphalus*, are known to be restricted to the Early Carboniferous, while six genera, *Paragoniozona*, *Eucochlis*, *Hemizyga* (*Hemizyga*), *Cyclozyga* and *Rhabdotocochlis* (herein identified), are previously recorded from Pennsylvanian strata of North America but not found in the Mississippian strata and correlatives outside Australia.

Table 1. Analyses of fossil molluscs (oxides) and number of ions calculated.

	<i>Knightsites</i> (<i>Retispira</i>)	<i>Eucochlis</i>	<i>Palaeozygopleura</i>	<i>Ianthinopsis</i>	<i>Nuculopsis</i>	<i>Plagioglypta</i>
	(%)	(%)	(%)	(%)	(%)	(%)
SiO ₂	28.29	28.78	28.67	27.73	29.18	27.94
Al ₂ O ₃	18.26	16.94	17.03	16.47	17.19	17.6
FeO	35.76	34.84	31.55	37.66	34.83	34.68
MgO	8.97	9.3	12.57	8.13	9.14	10.63
CaO	0.36	0.54	0.54	0.49	0.61	0.41
TOTAL	91.62	90.4	90.36	90.49	90.94	91.27
Number of ions						
Si	5.914 } 8	6.182 } 8	6.147 } 8	5.977 } 8	6.032 } 8	5.899 } 8
Al	2.086 } 8	1.818 } 8	1.853 } 8	2.023 } 8	1.968 } 8	2.101 } 8
Al	2.306 } 11.89	2.475 } 11.67	2.413 } 11.72	2.523 } 11.74	2.256 } 11.85	2.463 } 11.81
Fe+2	6.139 } 11.89	6.171 } 11.67	6.223 } 11.72	6.313 } 11.74	6.851 } 11.85	6.414 } 11.81
Mg	3.353 } 16	2.886 } 16	2.960 } 16	2.824 } 16	2.636 } 16	2.840 } 16
Ca	0.093 } 16	0.138 } 16	0.124 } 16	0.081 } 16	0.114 } 16	0.102 } 16
(OH)	16	16	16	16	16	16

Preservation

Nine specimens comprising seven gastropods, one bivalve and one scaphopod have been analysed by electron probing microanalyser. Table 1 shows the result of analyses and the number of ions which are calculated from the analyses on the basis of 28 oxygen equivalents, ignoring H₂O⁺, i.e., O₂₀(O,OH)₁₆ — the same approach as Deer, Howie & Zussman (1965). The percentage of oxides and number of ions of all specimens are similar and lie within the ranges of published chlorite analyses.

Two specimens (*Eucochlis* and *Nuculopsis*) have also been analysed by X-ray diffraction at the New South Wales Institute of Technology. The diffraction data, examined by Dr E. Slansky, represent peaks at 14, 7.1, 3.55 Å, indicating the presence of chlorite (and an admixture of quartz). This supports the conclusion, from electron microprobe analyses, that the fossils are chloritised. The specimens are generally greenish grey to dark grey in colour.

Chlorite replacement has made the isolation of complete shells from the limestone matrix possible and led to the preservation of delicate shell ornamentation. Thin minute shells are more perfectly preserved by chlorite replacement than big and thick shells. No macrospecimens have been isolated by acid digestion probably due to only partial replacement. Pyrite crystals are disseminated commonly in the chloritised shells.

Systematics

For systematic arrangement as well as the definition of genera, families and higher taxa, the Treatise on Invertebrate Paleontology, Part I — Mollusca 1 (chitons, scaphopods, gastropods), Part N — Mollusca 6 (pelecypods), and Part W — Miscellaneous (worms, conodonts, problematical fossils) was mainly consulted. To avoid repetition, only emended diagnoses are given in full in the systematic descriptions of taxa.

A systematic list of mollusc fauna from the investigated bioclastic limestone of the Dangarfield Formation is presented in Table 2.

C. GASTROPODA Cuvier, 1797

O. ARCHAEOGASTROPODA Theile, 1925

S.F. BELLEROPHONTACEA M'Coy, 1851

SINUITIDAE Dall, 1913

BUCANELLINAE Koken, 1925

Sinuitina Knight, 1945

Type species. *Tropidocyclus cordiformis* Newell, 1935: 349; from the Middle Pennsylvanian of Oklahoma.

Definition. See Knight *et al.*, 1960: 175.

Stratigraphic range. Silurian to Middle Permian.

Table 2. A systematic list of Mollusc Fauna from a bioclastic limestone in the Dangarfield formation. + = listed only; ° = listed and illustrated; * = illustrated and described in text.

Superfamily	Family	Genus, species and author	Fig.No.
Gastropoda			
Bellerophontacea	Sinuitidae	* <i>Sinuitina portulacoides</i> Campbell & Engel	1-3
		* <i>Euphemites</i> cf. <i>labrosa</i> Campbell & Engel	4-6
		* <i>sinuitid</i> n.gen.	7-8
	Bellerophontidae	* <i>Knightites</i> (<i>Retispira</i>) <i>culleni</i> Campbell & Engel	9-11
Macluritacea	Onychochilidae	* <i>Onychochilus minutissimus</i> n.sp.	12-14
Euomphalacea	Euomphalidae	° <i>Straparollus</i> (<i>Straparollus</i>) sp.	15-17
		+ <i>Straparollus</i> (<i>Serpulospira</i>) sp.	
Pleurotomariacea	Raphistomatidae	+ <i>Scalitina</i> sp.	
		* <i>Trepostira</i> (<i>Angiomphalus</i>) sp.	18-20
	Eotomariidae	° <i>Eotomaria</i> sp.	21-24
		* <i>Peruvipsira gundyensis</i> n.sp.	29-32
		+ <i>Spiroscala</i> sp.	
		* <i>Glabrocingulum obesum</i> n.sp.	33-35
		* <i>Hesperrella robertsi</i> n.sp.	36-41
	Lophospiridae	° <i>Worthenia</i> sp.	55-57
	Phymatopleuridae	* <i>Borestus costatus</i> n.sp.	25-28
		° <i>Paragoniozona</i> sp.	42-45
Platyceratacea	Holopeidae	* <i>Araonema microspirulata</i> n.sp.	46-49
		° <i>Rhabdotocochlis</i> sp.	50-51
		° "Rhabdotocochlis" sp.	52-54
	Platyceratidae	+ <i>Platyceras</i> sp.	
Microdomatacea	Microdomatidae	* <i>Microdoma angulata</i> n.sp.	58-60
	Elasmonematidae	* <i>Eucochlis australis</i> n.sp.	61-64
Neritacea	Neritopsidae	* <i>Naticopsis</i> (<i>Naticopsis</i>) <i>osbornei</i> n.sp.	65-66
		+ <i>Turbonitella</i> sp.	
Murchisoniacea	Murchisoniidae	* <i>Acisina turgida</i> n.sp.	80-81
		* <i>Stegocoelia</i> (<i>Stegocoelia</i>) <i>nodosa</i> n.sp.	67-71
		* <i>Stegocoelia</i> (<i>Hypergonia</i>) <i>elongata</i> n.sp.	73-75
		* <i>Stegocoelia</i> (<i>Hypergonia</i>) <i>tenuis</i> n.sp.	76-79
		° <i>Stegocoelia</i> (<i>Hypergonia</i>) sp.	72,82,83
Loxonematacea	Loxonematidae	* <i>Loxonema elegantissima</i> n.sp.	84-87
	Palaeozygopleuridae	+ <i>Palaeozygopleura</i> sp.	
	Pseudozygopleuridae	* <i>Hemizyga</i> (<i>Hemizyga</i>) <i>decussata</i> n.sp.	88-91
		* <i>Cyclozyga sinusigera</i> n.sp.	92-94
		+ <i>Microptychia</i> sp.	
Subulitacea	Subulitidae	+ <i>Ceraunocochlis</i> sp.	
		* <i>Soleniscus callosus</i> n.sp.	95-102
		° <i>Ianthinopsis</i> sp.	103
Pyramidellacea	Streptacidae	* <i>Donaldina filosa</i> n.sp.	104-109
		° <i>Donaldina</i> sp.	110-111
Bivalvia			
Nuculacea	Nuculidae	° "Nucula" sp.	112-117
		° "Nuculopsis" sp.	118-123
	Mallettiidae	° <i>Palaeoneilo acarinata</i> Campbell & Engel	124-125
Nuculanacea	Nuculanidae	+ <i>Phestia</i> sp.	
Pectinacea	Euchondriidae	+ <i>Euchondria</i> sp.	
Arcacea	Parallelodontidae	° <i>Parallelodon fossa</i> (Campbell & Engel)	126-127
		° <i>Edmondia</i> sp.	128-130
?Limopsacea		° n.gen. et n.sp.	131-133
?Modiomorphacea		° n.gen. et n.sp.	134-140
Scaphopoda	Dentaliidae	* <i>Fissidentalium?</i> <i>longistriatum</i> n.sp.	141-143
	Laevidentaliidae	* <i>Scissuradentalium runnegari</i> n.gen. et n.sp.	144-147
		* <i>Plagioglypta numerosa</i> n.sp.	148-151
		* <i>Pipadentalium protruberans</i> n.gen. et n.sp.	152-154
Hyolitha	Hyolithidae	* <i>Hyolithes minutissimus</i> n.sp.	155-162, 165
		° <i>Hyolithes</i> sp.	163-164

Australian Carboniferous species. *Sinuitina portulacoides* Campbell & Engel, 1963 seems to be the only described species from the Australian Carboniferous.

Sinuitina portulacoides Campbell & Engel

Figs 1–3

Sinuitina portulacoides Campbell & Engel, 1963: 90, pl. 6, figs 20–24.

Type material. Holotype (F.7573) and paratypes (F.7574–80) at the University of New England, Armidale, NSW.

Additional material examined. 32 specimens, from localities A–3 and C–34, 2.6 km south-west of Gundy, NSW.

Description. See Campbell & Engel, 1963: 90.

Dimensions. Fig. 2 (F.61940): largest diameter 2.42 mm, thickness of spire 1.52 mm. Fig. 3: largest diameter 1.56 mm, thickness of spire 1.43 mm.

Type locality. Namoi Formation; Swain's Gully and Rangari, 15 km south-west of Somerton and 37 km north-east of Gunnedah, respectively.

Stratigraphic range. Middle – Upper Tournaisian.

Remarks. Although the examined specimens are much smaller than the types, which are 16 mm in height, the present forms are similar to the types in shell character and regarded as a same species.

EUPHEMITINAE Knight, 1956

Euphemites Warthin, 1930

Type species. *Bellerophon urii* Fleming, 1828; from the Lower Carboniferous of Scotland.

Definition. See Knight *et al.*, 1960: 178.

Stratigraphic range. Lower Carboniferous to Permian.

Australian Carboniferous species. *Euphemites labrosa* Campbell & Engel, 1963, from Rangari, NSW; *Euphemites minutus* Maxwell, 1961: 62, pl. 7, figs 1–4 from Yarrol, Qld.

Euphemites labrosa Campbell & Engel

Figs 4–6

Euphemites labrosa Campbell & Engel, 1963: 91, pl. 6, figs 34–39

Type material. Holotype (F.7569) and paratypes (F.75701–72) at the University of New England, Armidale, NSW.

Additional material examined. 50 juvenile specimens from localities A–3, C–32 and C–34, 2.6 km south-west of Gundy, NSW.

Description. See Campbell & Engel, 1963: 91.

Dimensions. Fig. 4: largest diameter 108 mm, thickness of spire 1.00 mm; Fig. 5: largest diameter

1.14 mm, thickness of spire 1.10 mm; Fig. 6: largest diameter 1.76 mm, thickness of spire 1.36 mm.

Type locality. Near the top of the Tulcumba Sandstone, 1.5 km north-east of Rangari homestead, 37 km north-east of Gunnedah, NSW.

Stratigraphic range. Middle–Upper Tournaisian.

Remarks. The juvenile specimens recovered here have smaller shells with fewer spiral cords than the types. As they grow, cords increase by intercalation, and new ones rapidly attain normal size. The present form is tentatively regarded as conspecific as *E. labrosa* until an adult shell is recovered from the same locality.

BELLEROPHONTIDAE M'Coy, 1851

KNIGHTITINAE Knight, 1956

Knightites Moore, 1941

Knightites (Retispira) Knight, 1945

Type species. *Retispira bellireticulata* Knight, 1945: 335, pl. 49, figs la–c; from the Early Pennsylvanian age at the top of the Bend group of Texas.

Definition. See Knight *et al.*, 1960: 184.

Stratigraphic range. Devonian to Middle Permian.

Australian Carboniferous species. *Knightites (Retispira) culleni* Campbell & Engel seems to be the only figured species referred to this subgenus from the Australian Carboniferous.

Knightites (Retispira) culleni Campbell & Engel

Figs 9–11

Knightites (Retispira) culleni Campbell & Engel, 1963: 89, pl. 6, figs 27–33.

Type material. Holotype (F.7534) and paratypes (F.7535) at the University of New England, Armidale, NSW.

Additional material examined. 76 specimens from localities A–1, A–3 and C–34, 2.6 km south-west of Gundy, NSW.

Description. See Campbell & Engel, 1963: 89.

Dimensions. Fig. 9 (F.61943): largest diameter 3.04 mm, thickness of spire 3.60 mm; Fig. 10 (F.61943): largest diameter 1.20 mm, thickness of spire 1.18 mm; Fig. 11 (F.61943): largest diameter 1.45 mm, thickness of spire 1.60 mm; unfigured specimen: largest diameter 3.40 mm, thickness of spire 4.10 mm; unfigured specimen: largest diameter 4.36 mm, thickness of spire 5.60 mm; unfigured specimen: largest diameter 1.70 mm, thickness of spire 1.30 mm.

Type locality. Namoi Formation; Swain's Gully and Rangari, 15 km south-west of Somerton, and 37 km north-east of Gunnedah, respectively.

Stratigraphic range. Middle–Upper Tournaisian.

Remarks. The specimens examined are mostly

juvenile and are tentatively referred to this species. The specimens differ from the holotype, which possesses a short slit and thickened parietal inductura (Campbell & Engel, 1963: 90). One specimen (Fig. 9) with flared aperture has no slit. The slit may have disappeared as it attained maturity. *K. (R.) bellireticulata* Knight (1945) resembles the specimens, but differs in having a convex selenizone.

S.O. MACLURITINA Cox & Knight, 1960

S.F. MACLURITACEA Fischer, 1885

ONYCHOCHILIDAE Koken, 1925

ONYCHOCHILINAE Koken, 1925

Onychochilus Lindström, 1884

Type species. *Onychochilus physa* Lindström, 1884 (subsequent designation by Cossman, 1915: 252); from the uppermost limestone (bed c), Middle Silurian, Slite, Gotland, Sweden.

Definition. See Knight *et al.*, 1960: 187.

Remarks. The type species, *Onychochilus physa*, is reported to occur from the Middle Silurian Gotland, Sweden. The Australian form is very similar to the type species in shell character but different in being much smaller in shell size and lacks ornamentation. There are not enough significant differences to create a new genus.

***Onychochilus minutissimus* n.sp.**

Figs 12–14

Type material. Holotype (F.61944) and 3 paratypes (F.61945).

Additional material examined. 4 specimens.

Description. Shell minute, sinistral, pupiform, with smooth, convex whorls. Shell layer very thin; protoconch smooth, simple paucispiral. Sutures shallow, base slightly flattened with weak circumumbilical ridge, moderately phaneromphalous, lips of aperture thin, arcuate, outer lip opisthocline, straight without sinuosity, parietal lip narrow.

Dimensions. Holotype (Fig. 12): height 0.76 mm, width 0.54 mm, pleural angle 50°, number of whorls 3.75; paratype (Fig. 13): height 0.88 mm, width 0.54 mm, height of aperture 0.32 mm, pleural angle 45°, number of whorls 4.

Type locality. Locality A–4, 2.6 km south-west of Gundy, NSW.

Remarks. This is the only species referred to the genus *Onychochilus* in Australia, and appears to be the only post-Silurian record of the genus.

Etymology. Derived from the latin word *minutus* meaning lessened and *-issima* meaning superlative or extreme.

S.O. PLEUROTOMARIINA Cox & Knight, 1960

S.F. PLEUROTOMARIACEA Swainson, 1840

RAPHISTOMATIDAE Koken, 1896

LIOSPIRINAE Knight, 1956

Trepospira Ulrich & Scofield, 1897

Type species. *Pleurotomaria sphaerulata* Conrad, 1842: 272; from the Upper Carboniferous, “inclined plane of the Alleghany Mountain”, Pennsylvania, USA.

Definition. See Knight *et al.*, 1960: 201.

Stratigraphic range. Devonian to Middle Permian.

Trepospira (Angyomphalus) Cossman, 1916

Type species. *Euomphalus radians* de Koninck, 1843: 442, pl. 23, fig. 5; from the Lower Carboniferous of Tournai, Belgium.

Definition. See Knight *et al.*, 1960: 201.

Stratigraphic range. Lower Carboniferous.

Australian Carboniferous species. *Angyomphalus depressus* Campbell & Engel, 1963, from Rangari, NSW.

***Trepospira (Angyomphalus)* sp.**

Figs 18–20

Material examined. 32 juvenile specimens from locality A–3, 2.6 km south-west of Gundy, NSW.

Description. Shell small, low spired, lenticular form with 4.5 whorls. Protoconch seemingly simple, smooth. No sharp boundary between protoconch and teleoconch. Suture shallow; upper whorl face slopes gently toward periphery, decorated by narrow radiating nodes which are slightly sigmoidal just below suture. Growth lines extended beyond nodes, prosocline above selenizone which appears to be on periphery. Growth lines below selenizone faint, swinging forward for short distance, then backward into umbilicus. Columellar lip thin next to parietal wall but with thick subtriangular section at the circumumbilical funicle, outer lip thin, sharply angulated at periphery, size of slit and lunulae unknown, phaneromphalous.

Dimensions. Fig. 18 (F.61947): thickness of spire 1.40 mm, maximum diameter of spire 2.10 mm.

Remarks. This form is different from the only Australian species, *Trepospira (Angyomphalus) depressus* (Campbell & Engel) which has a lower spire, more acute periphery and a greater number of closely spaced, longer nodes just below the sutures. This form is similar to the Belgian type species *T. (A.) radians* (de Koninck) in shell character but differs in having smaller shell. All specimens here are juveniles and may be larger when fully grown.

EOTOMARIIDAE Wenz, 1938**EOTOMARIINAE** Wenz, 1938***Glabrocingulum*** Thomas, 1940

Type species. *Glabrocingulum beggi* Thomas, 1940: 38; from the Upper Calciferous Sandstone Series, Scotland.

Definition. See Thomas, 1940: 38.

Stratigraphic range. Lower Carboniferous to Middle Permian.

Remarks. *Mourlonia ornata* Dun & Benson, 1920 is now transferred to *Glabrocingulum*, because of its stronger spiral cords.

***Glabrocingulum obesum* n.sp.**

Figs 33–35

Type material. Holotype (F.61952) and 10 paratypes (F.61953).

Additional material examined. 10 specimens from localities A–4 and C–34.

Description. Shell small, conical turbiniform, with about 6 heavily ornamented convex whorls; suture moderately deep; base very convex, moderately phaneromphalous. Shell composed of 2 distinct layers; no distinct boundary between protoconch and teleoconch, first 1.5 whorls of neanic stage apparently showing faint growth lines. Selenizone, spiral and collabral cords start to occur on about second whorl, become gradually stronger. Spiral cords, 4 above selenizone, about 7 below selenizone; 30–34 collabral cords in last whorl. Spiral and collabral cords form distinct nodes at their intersections. Selenizone impressed, moderately wide, situated on the periphery. About 40 nodes in selenizone of last whorl. Collabral cords prosocline above selenizone but orthocline below it. Inner lip slightly reflected, outer lip thin with slit.

Dimensions. Holotype (Fig. 33): height 1.17 mm, width 1.47 mm, pleural angle 117°, number of whorls 3.5; paratype (Fig. 34): height 1.50 mm, width 1.45 mm, pleural angle 108°, number of whorls 4.

Type locality. Locality A–4, 2.6 km south-west of Gundy, NSW.

Remarks. This species is similar to the Scottish type species *Glabrocingulum beggi* Thomas in shell shape but different in having coarser ornamentation and a row of nodes in the selenizone. This species differs from *G. ornata* (Dun & Benson) in having much smaller and low-spired shell.

Etymology. Derived from the Latin word *obesus* meaning swollen.

AGNESIIDAE Knight, 1956***Hesperiella*** Holzapfel, 1889

Type species. *Pleurotomaria contraria* de Koninck, 1843; from Visé, Belgium.

Definition. See Knight *et al.*, 1960: 206.

Stratigraphic range. Lower Devonian to Upper Carboniferous.

Remarks. In this paper the genus *Hesperiella* is recorded for the first time in Australia, although species belonging to this genus have been discovered in many places in Europe. The coiling of shell and protoconch of *Hesperiella* is basically the same as in Recent species of Architectonicidae. The protoconch of both groups is inturned and the apex is seen through the umbilicus without change of coiling direction.

In the early embryonic stage, *Hesperiella* is dextrally coiled and Architectonicidae is sinistrally coiled, and immediately after the embryonic stage they change the direction of growth, not direction of coiling, viz. ultradextral in *Hesperiella* and ultrasinistral in Architectonicidae.

Knight (1941) suggested that this genus is a hyperstrophically coiled dextral shell. However the lack of a calcified operculum prevents the testing of this hypothesis (Batten, 1966).

***Hesperiella robertsi* n.sp.**

Figs 36–41

Type material. Holotype (F.61954) and 10 paratypes (F.61955).

Additional material examined. 33 specimens from localities A–3, A–4 and C–34.

Description. Shell small, sinistral, early whorls depressed completely, hidden by later whorls. First 1.75 planispiral smooth whorl including protoconch seen through umbilicus in broken shell. Teleoconch 3.5 whorls inflated, collabral cords from suture to selenizone weaker in early whorls, gradually stronger, more widely spaced with growth, 30–32 cords in last whorl. Selenizone seen only in last whorl, concave, distinct; no lunulae. Aperture nearly round, inner lip thick, reflected, base rather flat, more numerous fine collabral cords than present above selenizone, phaneromphalous.

Dimensions. Holotype (Fig. 36): height 3.30 mm, width 2.92 mm, height of aperture 1.48 mm, pleural angle 65°, number of whorls 3.5; paratype (Fig. 38): height 2.70 mm, width 2.45 mm, height of aperture 66°, number of whorls 3.5.

Type locality. Locality C–34, 2.6 km south-west of Gundy, NSW.

Remarks. This is the only known Australian species belonging to *Hesperiella*. There are two described European species, *H. thomsoni* (de Koninck) and *H. loudoni* Thomas. *H. thomsoni* has larger and more conical shell, while *H. loudoni* Thomas differs from *H. robertsi* n.sp. in being lower spired with more fine collabral cords.

Etymology. This species was named after Professor J. Roberts, University of New South Wales as an

acknowledgement of his contribution to the Carboniferous geology of the Hunter Valley District, NSW.

NEILSONIINAE Knight, 1956

Peruvispira J. Chronic, 1949

Type species. *Peruvispira delicata* J. Chronic, 1949; from Peru.

Definition. See Knight *et al.*, 1960: 207.

Stratigraphic range. Lower Permian to Middle Permian.

Australian Carboniferous species. *Peruvispira kempseyensis* Campbell, 1962, from Sherwood, 17 km west-north-west of Kempsey; *Peruvispira kuttungensis* Campbell, 1961, from the Booral Formation, south-eastern side of the Gloucester Trough, NSW.

Peruvispira gundyensis n.sp.

Figs 29–32

Type material. Holotype (F.61950) and 20 paratypes (F.61951).

Additional material examined. 38 specimens from localities A–3, A–4 and C–34.

Description. Shell small, globose, turbiniform, with 5.5 whorls. Protoconch changes gradually to teleoconch. First 2 whorls show fine spiral threads, prosocline growth lines; selenizone and collabral lirae first occur at third whorl. Collabral lirae, about 42–46 in the last whorl, evenly spaced, swinging backward above selenizone, orthocline below selenizone except for short forward segment just below lower margin of selenizone. Selenizone wide, slightly concave, with almost same number of curved lunules as collabral lirae. Aperture simple, columella straight, inner lip reflected, outer lip oblique from upper suture backward above selenizone; slit at selenizone; base rounded, moderately phaneromphalous.

Dimensions. Holotype (Fig. 29): height 2.80 mm, width 260 mm, pleural angle 65°, number of whorls 5.5; paratype (Fig. 31): height 3.16 mm, width 2.66 mm, pleural angle 65°, number of whorls 4.75; paratype (Fig. 30): height 2.22 mm, width 2.00 mm, pleural angle 67°, number of whorls 5.5; paratype (Fig. 32): height 2.12 mm, width 1.80 mm, pleural angle 65, number of whorls 5.

Type locality. Locality C–34, 2.6 km south-west of Gundy, NSW.

Remarks. This species differs from *P. kempseyensis* Campbell, 1962 and *P. kuttungensis* Campbell, 1961 in having smaller size of shell with a moderate umbilicus. *P. kempseyensis* has more closely spaced collabral lirae, while *P. kuttungensis* has taller spire and stronger collabral lirae.

Etymology. Referring to the geographical name of the township of Gundy, NSW.

PHYMATOPLEURIDAE Batten, 1956

Borestus Thomas, 1940

Type species. *Borestus wrighti* Thomas, 1940: 54, pl. 3, fig. 1a,b; from the Charlestown Main Limestone, Lower Limestone Group (P2), Roscobie Quarry, Fife, Scotland.

Definition. See Thomas, 1940: 53.

Stratigraphic range. Lower Carboniferous to Middle Permian.

Remarks. No Australian form has previously been referred to this genus.

Borestus costatus n.sp.

Figs 25–28

Type material. Holotype (F.61956) and 5 paratypes (F.61957).

Additional material examined. 9 specimens from localities A–3 and C–34.

Description. Shell small, conical trochiform, with about 5.75 heavily sculptured whorls, showing gradual change between protoconch and teleoconch, first 2 whorls nearly evenly spaced fine spiral threads with slightly prosocline, distinct growth lines. Selenizone and collabral lirae first occur at third whorl. Collabral ornament evenly spaced, regularly developed, about 36–40 cords in the last whorl; intersecting spiral cords at nodes, first at fourth whorl in median position above selenizone. Selenizone wide, deeply concave, its margins sharply keeled. Lunulae well developed, same number as collabral cords, J-shape. Base flat, reticulate ornamentation, moderately phaneromphalous.

Dimensions. Holotype (Fig. 25): height 3.00 mm, width 2.40 mm, apical angle 67°, number of whorls 6; paratype (Fig. 26): height 2.74 mm, width 2.00 mm, apical angle 70°, number of whorls 6.

Type locality. Locality C–34, 2.6 km south-west of Gundy, NSW.

Remarks. This is a very heavily ornamented form and is the first Australian species referred to this genus. This species resembles the Belgian species *B. similis* (de Koninck) but differs in being much smaller and in the detail of the ornamentation.

Etymology. Derived from the latin word *costatus* meaning costate, bearing ribs.

S.O. TROCHINA Cox & Knight, 1960

S.F. PLATYCERATACEA Hall, 1859

HOLOPEIDAE Wenz, 1938

GYRONEMATINAE Knight, 1956

Araeonema Knight, 1933

Type species. *Araeonema virgatum* Knight, 1933a: 52, pl. 9, fig. 3a–f; from the Labette Shale, Henrietta Formation, St. Louis, Missouri, USA.

Definition. See Knight, 1933: 40.

Stratigraphic range. Lower to Upper Carboniferous.

Remarks. This is the first record of the genus in Australia.

Araeonema microspirulata n.sp.

Figs 46–49

Type material. Holotype (F.61958) and 20 paratypes (F.61959).

Additional material examined. 43 specimens from A-3, A-4 and C-34.

Description. Shell minute, thin, globose, height slightly more than width of shell. Protoconch simple, boundary between protoconch and teleoconch not distinct, teleoconch about 3.5 convex whorls, first whorl smooth then equally spaced fine spiral lirae with fine orthocline growth lines. Suture deep, inner lip thin, gently arcuate, slightly reflected, outer lip orthocline without slit or selenizone, base round, moderately phaneromphalous.

Dimensions. Holotype (Fig. 46): height 1.07 mm, width 1.12 mm, height of aperture 0.67 mm, pleural angle 90°, number of whorls 4; paratype (Fig. 47): height 1.56 mm, width 1.48 mm, height of aperture 0.80 mm, pleural angle 85°, number of whorls 4.5.

Type locality. Locality A-4, 2.6 km south-west of Gundy, NSW.

Remarks. This species is superficially similar to *Araeonema virgatum* Knight (1933) described from St. Louis County, Missouri, USA., but differs in having a globose shell with a larger umbilicus and more inflated whorls with finer spiral lirae. This is the first species to be referred to the genus *Araeonema* in Australia.

Etymology. Referring to the microspiral ornamentation of shell.

S.F. MICRODOMATACEA Wenz, 1938

MICRODOMATIDAE Wenz, 1938

Microdoma Meek & Worthen, 1867

Type species. *Microdoma conicum* Meek & Worthen, 1867: 269; from the Carbondale Formation (Middle Pennsylvanian) Hodges Creek, Macoupin County, Illinois, USA.

Definition. See Knight *et al.*, 1960: 242.

Stratigraphic range. Lower Devonian to Lower Permian.

Remarks. No form has previously been referred to this genus in Australia.

Microdoma angulata n.sp.

Figs 58–60

Type material. Holotype (F.61960) and 20 paratypes (F.61961).

Additional material examined. 46 specimens from localities A-3, A-4, C-32 and C-34.

Description. Shell small, conical turbiniform, sutures deep, protoconch simple, rather globose 2.5 whorls, closely paced collabral threads, teleoconch of 2 whorls with uniformly strong collabral cords. Two strong spiral cords on last 2 whorls, one on periphery, the other just below suture. Collabral cords straight, prosocline, about 25° from vertical, evenly spaced but gradually wider with growth, 22–25 in last whorl, extending to umbilicus. Aperture subangular square in shape, inner lip thin nearly straight, raised, outer lip thin, prosocline, narrowly phaneromphalous.

Dimensions. Holotype (Fig. 58): height 2.20 mm, width 1.12 mm, height of aperture 0.76 mm, pleural angle 48°, number of whorls 5.25; paratype: height 1.84, width 1.24, height of aperture 0.78; paratype: height 2.20 mm, width 2.00 mm, height of aperture 0.90 mm; paratype: height 1.38, width 1.30 mm, height of aperture 0.68 mm; paratype (Fig. 59): height 2.20 mm; width 1.46 mm, pleural angle 50°, number of whorls 5.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This species is similar to *M. uniserrata* Batten (1966) described from the Hotwells Limestone, Compton Martin, England, in having flattened whorls and low periphery with strengthened collabral cords which form nodes. It differs in having a larger pleural angle and more numerous collabral cords.

Etymology. Derived from the latin word *angulatus* meaning angular.

ELASMONEMATIDAE Knight, 1956

Eucochlis Knight, 1933

Type species. *Eucochlis perminuta* Knight, 1933a: 41, pl. 9, fig. 2a-f (monotypy); from the Labette Shale, Henrietta Formation, St. Louis County, Missouri, USA.

Definition. See Knight, 1933: 40.

Stratigraphic range. Lower Carboniferous to Upper Carboniferous.

Remarks. This is the first record of the genus in Australia.

Eucochlis australis n.sp.

Figs 61–64

Type material. Holotype (F.61962) and 20 paratypes (F.61963).

Additional material examined. 160 specimens from localities A-3, A-4 and C-32.

Description. Shell minute, cyrtoclonoidal, rather short spired, protoconch 1.75 whorls with fine growth lines, teleoconch 2.5 strong convex with narrowly and evenly spaced sharp collabral cords, weak spiral lirae throughout teleoconch, collabral

cords about 43 in last whorl, prosocline, 26° from (vertical) axis and much more prominent than spiral lirae. Suture deep. Aperture simple, round. Lips slightly thickened, inner lip considerably separated from base abapically, moderately phaneromphalous.

Dimensions. Holotype (Fig. 61): height 1.28 mm, width 1.15 mm, height of aperture 0.65 mm, pleural angle 84°, number of whorls 4.25; paratype: height 1.13 mm, width 1.20 mm, height of aperture 0.60 mm; paratype (Fig. 62): height 1.45 mm, width 1.36 mm, height of aperture 0.70 mm, pleural 84°, number of whorls 3.75; paratype: height 1.20 mm, width 1.16 mm, height of aperture 0.66 mm.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. Knight (1933) described *Eucochlis perminuta* from St. Louis, Missouri, USA. The genus *Eucochlis* has remained monotypic until now, *australis* being the second species referred to the genus. *Eucochlis australis* is the most abundant and best preserved species in this study. It is superficially similar to *Eucochlis perminuta* in its size but differs in having a lower spire, bigger umbilicus, closer collabral cords and in being more conical.

Etymology. Derived from the latin word *australis* meaning southern.

S.O. NERITOPSINA Cox & Knight, 1960

S.F. NERITACEA Rafinesque, 1815

NERITOPSIDAE Gray, 1847

Naticopsis M'Coy, 1884

Naticopsis (*Naticopsis*) M'Coy, 1844

Type species. *Naticopsis phillipsii* M'Coy, 1844: 33 (subsequent designation by Meek & Worthen, 1866: 364); from the "Lower Limestone", Lower Carboniferous of Kilcommock, Longford, Ireland.

Definition. See Knight *et al.*, 1960: 276.

Stratigraphic range. Middle Devonian to Triassic.

Australian Carboniferous species. *Naticopsis brevispira* (Ryckholt, 1847), Dun & Benson, 1920 (361, pl. 22, fig. 8) from Carroll, NSW; *Naticopsis globosa* (Hoeninghaus, 1829), Dun & Benson, 1920 (361, pl. 22, figs 15,16) from south-east of Babbinsboon, NSW; *Naticopsis obliqua* Dun & Benson, 1920 (362, pl. 22, figs 13,14) from south-east of Babbinsboon, NSW.

Naticopsis (*Naticopsis*) *osbornei* n.sp.

Figs 65-66

Type material. Holotype (F.61964) and 10 paratypes (F.61965).

Additional material examined. 3 specimens from locality A-3.

Description. Shell small, subglobular, neritopsid form with about 4 whorls, protoconch about 1.25

smooth, rounded whorls, teleoconch inflated, whorls embrace much of previous whorl, last 2 whorls ornamented by fine prosocline collabral threads displayed from suture to columellar region. Upper whorl surface flattened, with low subangular periphery. Columellar lip arcuate, parietal wall thickened with inductura which is crossed obliquely by 3 transverse rugae in parietal region, outer lip sharp and thin, anomphalous.

Dimensions. Holotype (Fig. 65): height 2.25 mm, width 2.20 mm, pleural angle 118°, number of whorls 4; paratype (Fig. 66): height 2.20 mm, width 2.10 mm, pleural angle 117°, number of whorls 4.5.

Type locality. Locality C-34, 2.6 km south-west of Gundy, NSW.

Remarks. This species resembles Belgian species *Naticopsis* (*Naticopsis*) *consimilis* de Koninck in shell ornamentation but differs in having a taller spire and thicker parietal wall. The Australian species, *N. brevispira*, has a more globose and larger shell; *N. globosa* may have no collabral threads; *N. obliqua* has a much taller shell.

Etymology. This species is named after Dr G.D. Osborne, formerly of the University of Sydney for his contribution to geology of Muswellbrook-Scone District which includes the present study area.

S.O. MURCHISONIINA Cox & Knight, 1960

S.F. MURCHISONIACEA Koken, 1896

MURCHISONIIDAE Koken, 1896

Aclisina de Koninck, 1881

Type species. *Murchisonia striatula* de Koninck, 1843: 415, pl. 40, figs 7a,b (subsequent designation by S.A. Miller, 1889: 395); from the V₃b(=D₂) zone, Visé, Belgium.

Definition. See Knight *et al.*, 1960: 293.

Stratigraphic range. Lower Carboniferous to Upper Carboniferous.

Remarks. This is the first record of *Aclisina* in Australia.

Aclisina turgida n.sp.

Figs 80-81

Type material. Holotype (F.61966) and 15 paratypes (F.61967).

Additional material examined. 10 specimens from localities A-3 and C-32.

Description. Shell small, relatively low spired, globose form, whorl profile rounded, suture deeply incised, protoconch 1 smooth whorl, teleoconch about 5 whorls with 6 evenly spaced spiral costae. Aperture subcircular, but slightly higher than wide, inner lip slightly arcuate, outer lip thin, convex, slit unknown may be small and narrow, giving rise to an obscure selenizone, anomphalous.

Dimensions. Holotype (Fig. 80): height 2.12 mm,

width 1.00 mm, height of aperture 0.74 mm, pleural angle 35°, number of whorls 5.5.

Type locality. Locality C-34, 2.6 km south-west of Gundy, NSW.

Remarks. The slit and selenizone are not clearly observed in the holotype, seemingly not a mature form. The other specimen (Fig. 81) is also juvenile, having few whorls but same pleural angle (35°) as the holotype. This is the first species to be referred to *Aclisina* in Australia.

Etymology. Derived from the latin word *turgidus* meaning swollen.

Stegocoelia Donald, 1889

Stegocoelia (*Stegocoelia*) Donald, 1889

Type species. *Murchisonia* (*Stegocoelia*) *compacta* Donald, 1889: 624, pl. 20, figs 9-13; from the Upper limestone series (Lower Carboniferous), Glencart, Dalry, Scotland.

Definition. See Knight *et al.*, 1960: 293.

Stratigraphic range. Lower Carboniferous to Upper Carboniferous.

Remarks. No Australian form has previously been referred to the genus *Stegocoelia*.

Stegocoelia (*Stegocoelia*) *nodosa* n.sp.

Figs 67-71

Type material. Holotype (F.61968) and 20 paratypes (F.61969).

Additional material examined. 150 specimens from A-3, A-4, C-32 and C-34.

Description. Shell small, relatively thick, tall spired, whorl profile convex. Protoconch 2 smooth whorls its labral sinus culminating in a sharp notch in periphery (see Fig. 71); teleoconch 5 whorls with 4 strong spiral carinae with fine orthocline growth lines. One spiral carina abapical to suture weaker than other 3, but has about 2-30 nodes in last whorl. Aperture simple, inner lip thin, slightly arcuate, reflexed, outer lip shallow opisthocyst just below suture, slit absent or seemingly very shallow, selenizone obscured between second and third carinae below suture, anomphalous.

Dimensions. Holotype (Fig. 68): height 2.40 mm, width 1.00 mm, height of aperture 0.58 mm, pleural angle 20°, number of whorls 7.5; paratype (Fig. 70): height 2.76 mm, width 1.06 mm, pleural angle 22°, number of whorls 7; paratype (Fig. 67): height 2.42 mm, width 0.92mm, pleural angle 22°, number of whorls 6.5.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This is one of the most common species in the investigated fauna. *S. (S.) nodosa* is very similar to *S. (S.) okawensis* Thein & Nitecki (1974) from Upper Mississippian of Illinois Basin, North

America in the form of the shell and type of ornamentation, but is different in having nodes on the upper spiral cords.

Etymology. Derived from the latin word *nodosus* meaning nodose, referring to nodes on the upper spiral cords.

Stegocoelia (*Hypergonia*) Donald, 1892

Type species. *Murchisonia* *quadracarinata* M'Coy, 1844: 42, pl. 5, fig. 9; from the Carboniferous limestone of Blacklion, Enniskillen, Northern Ireland.

Definition. See Knight *et al.*, 1960: 293.

Stratigraphic range. Lower Carboniferous to Upper Carboniferous.

Stegocoelia (*Hypergonia*) *elongata* n.sp.

Figs 73-75

Type material. Holotype (F.61970) and 14 paratypes (F.61971).

Additional material examined. 7 specimens from locality C-32.

Description. Shell small, high spired, turriculate with flattened base, whorl profile rather flat, suture shallow. Protoconch 1 smooth whorl, prominent varix between protoconch and teleoconch forming deep labral sinus culminating in sharp notch in upper part of whorl; teleoconch about 8 whorls with 4 strong spiral carinae of which 2 middle carinae being stronger than those above and below. Slit seemingly shallow selenizone obscure between 2 uppermost carinae. Aperture almost square in shape, outer lip with slight angulations both anteriorly and posteriorly. Growth lines very faint, swing moderately backward above selenizone, forward between selenizone and lower suture, backward on base, anomphalous.

Dimensions. Holotype (Fig. 73): height 3.76 mm, width 1.30 mm, height of aperture 0.68 mm, pleural angle 19°, number of whorls 9.25.

Type locality. Locality A-4, 2.6 km south-west of Gundy, NSW.

Remarks. This species resembles *Stegocoelia* (*Hypergonia*) *cincta* (Donald, 1895) from the Upper Limestone Group (=E2) of Ayrshire, but differs in that *S. (H.) cincta* has a more coeloconoid form.

Etymology. Derived from the latin word *elongatus* meaning elongate, referring to the tall spire of shell.

Stegocoelia (*Hypergonia*) *tenuis* n.sp.

Figs 76-79

Type material. Holotype (F.61972) and 12 paratypes (F.61973).

Additional material examined. 3 specimens from locality C-32.

Description. Shell minute, slender, tall spired, turritelliform with round base, shell profile rounded,

suture deeply incised. Protoconch about 2 smooth whorls, labral sinus culminating in sharp notch in upper part of whorl; teleoconch about 7 whorls with 3 distinct spiral cords consistently in lower half of whorl. Selenizone may be along the groove which is just below suture. Growth lines faint, slightly backward above groove, forward strongly below groove. Slit unknown. Aperture round, inner lip arcuate, slightly reflected, anomphalous.

Dimensions. Holotype (Fig. 76): height 1.10 mm, width 0.35 mm, pleural angle 15°, number of whorls 8; paratype (Fig. 77): height 1.07 mm, width 0.32 mm, pleural angle 14°, number of whorls 8.5.

Type locality. Locality A-4, 2.6 km south-west of Gundy, NSW.

Remarks. This species is somewhat similar to *Donaldina filosa* n.sp. in shell size and teleoconch ornamentation but very different in the nature of its protoconch and the sharp notch between protoconch and teleoconch. Fine meandering grooves on the shell surface, which may have been caused by algae or bacteria, are common, particularly on the protoconch.

Etymology. Derived from the latin word *tenuis* meaning thin, slender, referring to the slender shell shape.

O. CAENOGASTROPODA Cox, 1959

S.F. LOXONEMATACEA Koken, 1889

LOXONEMATIDAE Koken, 1889

Loxonema Phillips, 1841

Type species. *Terebra? sinuosa* J. de C. Sowerby, 1839 (subsequent designation, King, 1850: 209); from Middle Silurian, near Aymestry, Shropshire, England.

Definition. See Knight *et al.*, 1960: 311.

Stratigraphic range. Middle Ordovician to Lower Carboniferous.

Australian Carboniferous species. *Loxonema babbinboonensis* Etheridge Jr., 1907 (194, pl. 38, figs 5,6), from Babbinboon; *Loxonema lamellosa* Maxwell, 1961 (69, pl. 9, figs 6-11), from late Tournaisian-early Visean, Yarrol, Qld; *Loxonema* sp. Dun & Benson, 1920 (362, pl. 22, figs 11,12), from Babbinboon; *Loxonema* sp. (cf. *lefevrei*) Etheridge Jr. 1907 (195, pl. 37, figs 4,5); *Loxonema acutissima* de Koninck, *L. constricta* W. Martin, *L. difficilis* de Koninck, and *L. rugifera* J. Phillips (all figured in de Koninck, 1898) do not seem to be *Loxonema*.

Loxonema elegantissima n.sp.

Figs 84-87

Type material. Holotype (F.61974) and 10 paratypes (F.61975).

Additional material examined. 16 specimens from A-3, A-4 and C-34.

Description. Shell minute, slender, high spired, 7-9 whorls, whorl profile rounded, sutures deep. Protoconch simple, rather slightly deviated 1.25 smooth whorls; teleoconch about 6-8 convex whorls with very fine collabral cords. Collabral cords pass obliquely backward from upper suture at an angle of about 40° to axis of shell, forward sharply across whole lower face of whorl at an angle of about 30° to axis. Aperture oval, inner lip slightly arcuate, outer lip thin, with deep rounded labral sinus culminating high on whorl; base round, anomphalous.

Dimensions. Holotype (Fig. 84): height 1.36 mm, width 0.50 mm, height of aperture 0.32 mm, pleural angle 15°, number of whorls 6.5; paratype (Fig. 85): height 2.50 mm, width 0.70 mm, height of aperture 0.44 mm, pleural angle 13°, number of whorls 7.5.

Type locality. Locality A-4, 2.6 km south-west of Gundy, NSW.

Remarks. *Donaldina filosa* n.sp. is similar to this species in shell shape but different in having spiral cords and a more blunt topped protoconch. *L. elegantissima* n.sp. is similar to *Donaldina* sp. (Figs 110, 111) but *Donaldina* sp. has a more deviated protoconch and spiral cords.

Bored holes appear on the shell as in *Stegocoelia* (*Hypergonia*) *tenuis* n.sp. Their size suggests that they are caused by algae or bacteria, not by molluscan predators.

Etymology. Derived from the latin word *elegantissimus* meaning most elegant.

PSEUDOZYGOPLURIDAE Knight, 1930

Hemizyga Girty, 1915

Hemizyga (*Hemizyga*) Girty, 1915

Type species. *Hemizyga elegans* Girty, 1915: 362, pl. 32, figs 7A, B; from the Cherokee Shale (Upper Carboniferous) on Honey Creek, Garland, Missouri, U.S.A. Subsequent designation Knight, 1930: 17.

Definition. Shell very small, cyrtocoenoidal fusiform, anomphalous, high spired but relatively few whorls, with extremely fine collabral costae or lirae, base rather extended subconical, aperture somewhat elongate auriform, protoconch 3-4 whorls with fine reticulate sculpture (emend.).

Stratigraphic range. Lower to Upper Carboniferous.

Remarks. No Australian form has previously been referred to the family Pseudozygopleuridae and its genera.

Hemizyga (*Hemizyga*) *decussata* n.sp.

Figs 88-91

Type material. Holotype (F.61976) and 5 paratypes (F.61977).

Additional material examined. 5 specimens from locality C-34.

Description. Shell minute, cryptoconoidal fusiform, whorl profile gently arched, with rapidly increasing, last whorl very much inflated. Sutures shallow, protoconch 4.25 whorls, first 1.75 whorls smooth, rest 2.5 whorls strong decussate ornamentation, gradually transformed into teleoconch pattern; teleoconch about 2 whorls with straight orthoconal collabral cords which extend onto base. Aperture elongate auriform, inner lip thick, reflexed; outer lip thin, no sinus, arcuate; lower lip extended, siphonate; anomphalous.

Dimensions. Holotype (Fig. 88): height 2.00 mm, width 1.45 mm, height of aperture 1.20 mm, pleural angle 56°, number of whorls 4+; paratype: height 1.72 mm, width 1.20 mm, height of aperture 0.74 mm; veliger shell (Fig. 89): height 0.90 mm, width 0.61 mm, height of aperture 0.40 mm.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This is the first Australian species referred to the genus *Hemizyga* (*Hemizyga*).

Etymology. Derived from the latin word *decusso* meaning to divide crosswise in the shape of an X.

Cyclozyga Knight, 1930

Type species. *Cyclozyga mirabilis* Knight, 1930: 74, pl. 5, fig. 7; from the top of the Labette Shale, Henrietta Formation, St. Louis County, Missouri, USA.

Definition. Shell minute, protoconch first 1-1.5 whorls smooth, strong collabral ornament on 2nd to 4th whorls, spiral threads on adult shell, shallow sinus low on whorl (emend.).

Stratigraphic range. Lower to Upper Carboniferous.

Cyclozyga sinusigera n.sp.

Figs 92-94

Type material. Holotype (F.61978) and 1 paratype (F.61979).

Additional material examined. 2 specimens.

Description. Shell minute, slender, moderately high spired, whorls rounded, sutures moderately deep, protoconch 2.5 whorls, first 1 whorl smooth, blunt, rest 1.5 whorls strong collabral cords shown, abrupt change to teleoconch with exceptionally deep sinus of a peculiar deep-U shape; teleoconch about 4.5 whorls with 3-4 equal spiral cords, all equally spaced, confined generally to lower part of whorl, fine collabral threads inclined obliquely backward below suture but immediately turned forward with an angle of 30° to axis of shell; inner lip arcuate, somewhat reflexed, outer lip thin but not well known in detail, base flat, anomphalous.

Dimensions. Holotype (Fig. 92): height 1.45 mm, width 0.50 mm, height of aperture 0.32 mm, pleural angle 20°, number of whorls 7.5; paratype (Fig. 93):

height 0.82 mm, width 0.40 mm, height of aperture 0.20 mm, pleural angle 22°, number of whorls 6+.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This species differs from the other known three congeneric species, *C. mirabilis* Knight (1930), *C. carinata* Knight (1930) and *C. attenuata* Hoare & Sturgeon (1978), all from the Pennsylvanian of USA, in having a much smaller and more slender shell, and also in having strongly oblique opisthocline growth lines. This species is rare in the fauna described in this paper, but is well preserved although the later whorls of the paratype are slightly damaged. The high-spired larval shell with deep sinus indicates that this species had a planktotrophic development.

Etymology. Derived from the latin words *sinus* meaning a curve, and *gero* meaning to bear; referring to the shape of the protoconch.

S.F. SUBULITACEA Lindström, 1884

SUBULITIDAE Lindström, 1884

SOLENISCINAE Wenz, 1938

Soleniscus Meek & Worthen, 1861

Type species. *Soleniscus typicus* Meek & Worthen, 1861; Upper Carboniferous, from Springfield, Illinois, USA.

Definition. See Knight *et al.*, 1960: 321.

Stratigraphic range. Lower Carboniferous to Middle Permian.

Soleniscus callosus n.sp.

Figs 95-102

Type material. Holotype (F.61980) and 7 paratypes (F.61981).

Additional material examined. 12 specimens from A-4 and C-34.

Description. Shell small, moderately high spired fusiform but shell profile slightly concave; whorl profile gently rounded, suture shallow, distinct; protoconch of small size, simple; teleoconch with fine transverse lirae, last whorl markedly inflated, 2 times as high as preceding spire. Aperture suboval, pointed posteriorly, rounded anteriorly; outer lip thin, arcuate; columellar lip slightly arcuate, with small siphonal notch, strong columellar fold internally in last 2 whorls; parietal inductura slightly thickened, base round, anomphalous.

Dimensions. Holotype (Fig. 100): height 1.80 mm, width 1.00 mm, pleural angle 52°, number of whorls 6; paratype (Fig. 101): height 1.50 mm, width 1.00 mm, pleural angle 56°, number of whorls 5+; paratype (Fig. 96): height 1.43 mm, width 0.86, pleural angle 50°, number of whorls 5.5; paratype (Fig. 97): height 1.80 mm, width 1.10 mm, pleural angle 55°, number of whorls 5.5; paratype (Fig. 98):

height 2.50 mm, width 1.50 mm, pleural angle 53°, number of whorls 5.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This is a very common species in the fauna here described. It displays a striking amount of variability in shell shape, whorl profile, ornament and columellar lip.

Etymology. Derived from the latin word *callosus* meaning calloused, referring to the columellar callus.

S.C. OPISTHOBRANCHIA Milne Edwards, 1848

O. Uncertain

S.F. PYRAMIDELLACEA d'Orbigny, 1840

STREPTACIDIDAE Knight, 1931

Donaldina Knight, 1933

Type species. *Aclisina grantonensis* Donald, 1898: 60, pl. 4, figs 7-9; from the Calciferos Sandstone Group, at Woodhall, near Edinburgh, Scotland.

Definition. See Knight *et al.*, 1960: 322.

Stratigraphic range. Devonian? Lower Carboniferous to Lower Permian.

Remarks. This genus is introduced for the first time to the Australian fauna to accommodate *Donaldina filosa* n.sp. and *Donaldina* sp.

Donaldina filosa n.sp.

Figs 104-109

Type material. Holotype (F.61982) and 20 paratypes (F.61983).

Additional material examined. 9 specimens from localities A-3 and C-34.

Description. Shell minute, slender, high spired turriculate form. Whorl profile between sutures more or less symmetrically rounded, sutures deep, well impressed. Protoconch of 1.5 smooth whorls with flat top to slightly submerged spire. Varix between protoconch and teleoconch distinct orthocline, teleoconch about 8 convex whorls with 5-6 evenly spaced spiral cords and closely spaced collabral threads. Spiral ornamentation confined generally to lower $\frac{2}{3}$ of each whorl. Collabral threads deflected strongly backward below suture but swinging immediately and strongly forward with an angle of 25° to axis of shell. Aperture oval, columellar lip slightly arcuate, base rounded, anomphalous.

Dimensions. Holotype (Fig. 105): height 1.77 mm, width 0.50 mm, pleural angle 14°, number of whorls 9; paratype (Fig. 104): height 1.66 mm, width 0.55 mm, pleural angle 15°, number of whorls 7.5.

Type locality. Locality A-4, 2.6 km south-west of Gundy, NSW.

Remarks. This species is very similar to *Loxonema elegantissima* n.sp. in shell size, shape, protoconch

and strong opisthocline collabral ornamentation but different from it in having spiral cords. This species is also similar to *Donaldina* sp. but that form has a more deviated protoconch.

Etymology. Derived from the latin word *filosus* meaning threaded, bearing threads.

C. SCAPHOPODA Bronn, 1862

O. DENTALIOIDA Palmer, 1974

DENTALLIIDAE Gray, 1834

Fissidentalium Fischer, 1885

Type species. *Dentalium ergasticum* Fischer, 1882; Recent, Gulf of Gascony and Atlantic Ocean, in deep water.

Definition. Shell large, solid, circular in outline, sculptured with numerous longitudinal striae; apex typically with long apical fissure on convex side, rarely simple or with apical slit divided into a series of fissures (Emerson, 1962).

Stratigraphic range. ?Early Carboniferous; Cretaceous to Recent.

Remarks. The present two specimens resemble *Prodentalium* in having fine longitudinal riblets extending seemingly the entire length of tube, but differ in that *Prodentalium* is a very large scaphopod, 20 cm long, without observed slit or plug. The Recent genus *Fissidentalium* resembles those present specimens in having fine longitudinal riblets and long apical slit (Palmer, 1974), but differs in being a long tube, reaching 10 cm long. The size of complete tubes are not known as both specimens recovered here have the anterior part damaged. Therefore the present specimens are tentatively referred to *Fissidentalium*.

Fissidentalium? longistriatum n.sp.

Figs 141-143

Type material. Holotype (F.61992) and 1 paratype (F.61993).

Additional material examined. 2 specimens.

Description. Shell minute, nearly straight, circular in section, surface sculptured with numerous close very fine longitudinal riblets extending seemingly entire length of tube, posterior orifice round with relatively long, narrow apical slit.

Dimensions. Holotype (Fig. 141): length 3.00 mm, diameter of anterior end 0.80 mm; paratype: length 2.50 mm, diameter of anterior end 0.60 mm.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This is the first record of a Palaeozoic species referred to this genus.

Etymology. Derived from the latin word *longus* meaning long, and *striatus* meaning striated.

LAEVIDENTALIIDAE Palmer, 1974

Scissuradentalium n.gen.

Type species. *Scissuradentalium runnegari* n.sp. (monotypy).

Definition. Shell minute to small (up to 7 mm long), slightly curved, with circular or nearly circular cross section, exterior and interior surfaces smooth, rapidly tapering posteriorly; very long, narrow apical slit on ventral side.

Stratigraphic range. Lower Carboniferous.

Remarks. *Scissuradentalium* n.gen. resembles *Rhytidentalium* Pojeta & Runnegar (1979) in having a slightly curved smooth shell, but differs in having a very long, narrow apical slit. This genus is similar to *Pseudantalis* Monterosato, which ranges from Lower Cretaceous to Recent, in having a smooth shell with long apical slit, but *Pseudantalis* differs in having a large, less tapering shell. *Scissuradentalium* may be an ancestor of *Pseudantalis* and could have evolved from *Rhytidentalium*.

Etymology. Derived from the latin word *scissura* meaning a slit, referring to the character of the posterior end; *Dentalium*, a genus of scaphopods.

Scissuradentalium runnegari n.sp.

Figs 144–147

Type material. Holotype (F.61994) and 8 paratypes (F.61995).

Additional material examined. 9 specimens.

Description. Shell small, rather short, slightly curved, rapidly attenuated posteriorly. Shell smooth, composed of 2 layers. Anterior aperture large, round; posterior aperture small, round, with very long, narrow apical slit on ventral side.

Dimensions. Holotype (Fig. 144): length 6.2 mm, diameter of anterior end 1.7 mm; paratype (Fig. 147): length 7 mm, diameter of anterior end 2 mm; paratype (Fig. 145): length 5.5 mm, diameter of anterior end 1.4 mm.

Type locality. Locality A–3, 2.6 km south-west of Gundy, NSW.

Remarks. This species differs from any other known Palaeozoic scaphopod from Australia or overseas.

Etymology. This species is named after Professor B. Runnegar of the University of New England for his contributions to the study of Australian Palaeozoic molluscs.

Plagioglypta Pilsbry & Sharp, 1897

Type species. *Dentalium undulatum* Münster, 1844; from Triassic, St. Cassian, Tyrol Mountains.

Definition. See Ludbrook, 1960: 39.

Stratigraphic range. Upper Devonian to Upper Cretaceous.

Remarks. The Australian forms of this genus appear to be so similar that they may be considered congeneric with the northern hemisphere counterparts.

Plagioglypta numerosa n.sp.

Figs 148–151

Type material. Holotype (F.61996) and 20 paratypes (F.61997).

Additional material examined. 30 specimens from localities A–3, A–4 and C–34.

Description. Shell small, slightly curved, slightly attenuate posteriorly. Shell surface throughout shows close but rather strong oblique wrinkles encircling whole shell, no longitudinal sculpture. Wrinkles sometimes rhythmically change from coarse to fine. Circular in cross section, slit and pipe absent.

Dimensions. Holotype (Fig. 148): length 3.60 mm, diameter of anterior end 0.76 mm; paratype (Fig. 149): length 3.30 mm, diameter of anterior end 0.72 mm.

Type locality. Locality A–3, 2.6 km south-west of Gundy, NSW.

Remarks. This is the first species to be referred to this genus in Australia.

Etymology. Derived from the latin word *numerosus* meaning rhythmical, alluding to the rhythmic change in size and frequency of the transverse wrinkles.

Pipadentalium n.gen.

Type species. *Pipadentalium protruberans* n.sp. (monotypy).

Definition. Shell minute, tapering (up to 6 mm long), slightly curved with loosely and smoothly encircling wrinkles, very fine longitudinal riblets throughout shell. Posterior orifice a distinct pipe.

Stratigraphic range. Lower Carboniferous.

Remarks. This genus resembles *Plagioglypta* Pilsbry & Sharp, 1897 in having encircling wrinkles but differs in having a distinct apical pipe and very fine longitudinal riblets.

Etymology. Derived from the latin word *pipare* meaning a tube, referring to the siphonal pipe at the posterior end; *Dentalium*, a genus of scaphopods.

Pipadentalium protruberans n.sp.

Figs 152–154

Type material. Holotype (F.61998) and 1 paratype (F.61999).

Additional material examined. 2 specimens.

Description. Shell small, slightly curved, slightly

attenuated posteriorly, shell surface loosely and slightly oblique wrinkled, showing very fine longitudinal riblets throughout. Circular in cross section, pipe at posterior end.

Dimensions. Holotype (Fig. 152): length 6.2 mm, diameter of anterior end 1.0 mm.

Type locality. Locality A-3, 2.6 km south-west of Gundy, NSW.

Remarks. This species is so similar to *Plagioglypta numerosa* n.sp. in shell size and shape that it can be confused when the specimen has the apical pipe broken off. Its characteristics are the apical pipe and faint encircling wrinkles with fine longitudinal lirae.

Etymology. Derived from the latin word *protruberans* meaning protruding, referring to the protruding apical pipe.

C. HYOLITHA Matthew, 1899

O. HYOLITHIDA Matthew, 1899

HYOLITHIDAE Nicholson, 1872

Hyolithes Eichwald, 1840

Type species. *Hyolithes acutus* Eichwald, 1840: 97; from Ordovician, Estonia.

Definition. See Fisher, 1962: 124.

Stratigraphic range. Lower Cambrian to Middle Permian.

Hyolithes minutissimus n.sp.

Figs 155-162, 165

Type material. Holotype (F.62000) and 10 paratypes (F.62001).

Additional material examined. 10 specimens from locality C-32.

Description. Shell minute; bilaterally symmetrical with straight or slightly curved, subtriangular cross section, embryonic portion smooth globular, sharply delimited from main part of shell; inside of embryonic chamber simple hole, wider in middle and top end than lower part of chamber, no septum between embryonic chamber and rest of shell. Shell next to embryonic chamber cylindrical but becoming subtriangular in cross section. Exterior and interior surfaces are ornamented by fine transverse striae which are coarser on exterior than interior. Lip extended from ventral side of aperture, transverse ornamentation on ventral side arched. Aperture subtriangular; operculum and arms unknown.

Dimensions. Holotype (Fig. 157): length 3.60 mm, maximum width 1.08 mm; paratype (Fig. 155): length 3.52 mm, maximum width 1.00 mm.

Type locality. Locality C-34, 2.6 km south-west of Gundy, NSW.

Remarks. The specimens recovered here are consistently small, ranging from 3 to 6 mm long, and

the ratio of protoconch length to teleoconch averages 1:20, which may indicate the attainment of maturity. This species differs from all other Palaeozoic hyolith species in having much smaller size of shell. This is the only Carboniferous species found in Australia.

Etymology. Derived from the latin word *minutus* p.p. of *minuere*, meaning lessen, and *-issima* meaning superlative or extreme.

Discussion

Large molluscan faunas have been described from the British Isles, Europe and North America. However, only a small number of species have been described from the Australian Carboniferous sediments.

During the present study, the largest assemblage of Carboniferous mollusc faunas (with other groups of marine faunas), was discovered in a bioclastic limestone lens interbedded in mudstone of the Dangarfield Formation. The limestone is interpreted to have formed in a shallow marine shelf environment. The limestone lens extends 800 m in a northwest-southeast direction, and consists of three thin bands of limestone ranging in thickness from 0.1 to 0.2 m. In this paper, gastropods, scaphopods and hyoliths are systematically classified. This mollusc assemblage (56 species including unidentified forms) is also the largest to be recovered from a single locality in Australian Palaeozoic rocks.

The faunal assemblage consists almost entirely of minute shells preserved by chlorite replacement, which has made possible the isolation of complete shells from the limestone matrix, and has led to the preservation of extremely delicate shell ornamentation.

While Recent and Tertiary micro-molluscs have received much attention in recent years, very little was known of the Australian pre-Tertiary minute molluscs. Systematic studies suggest that a large assemblage of macro- and micro-molluscs existed in the Early Carboniferous of Australia.

Thirty-four genera and subgenera of gastropods identified in this study were originally named in the British Isles-Europe and/or North America. Most of them occur in both continents. Only four genera occurring in Australia and Europe have not been found in North America, and another four genera occurring in Australia and North America have not been found in Europe. There are no endemic genera. The Australian fauna is a mixture of both European and North American affinities, of which some are restricted to the Early Carboniferous period. This agrees with the conclusion of Roberts (1987) that the Early Carboniferous marine invertebrate faunas of the Tasman Belt in Eastern Australia are cosmopolitan.

Correlations of conodont, ammonoid, brachiopod and other groups of marine assemblage from the study area with those of North America and Europe

suggest consistently that the sequence correlates with the Late Tournaisian (Early Carboniferous) of Europe.

Some species in the assemblage are recognised as typical planktotrophic gastropods which have potential dispersal ability for a wide geographical distribution. Lecithotrophic gastropods are also found. These gastropods have reduced dispersal ability.

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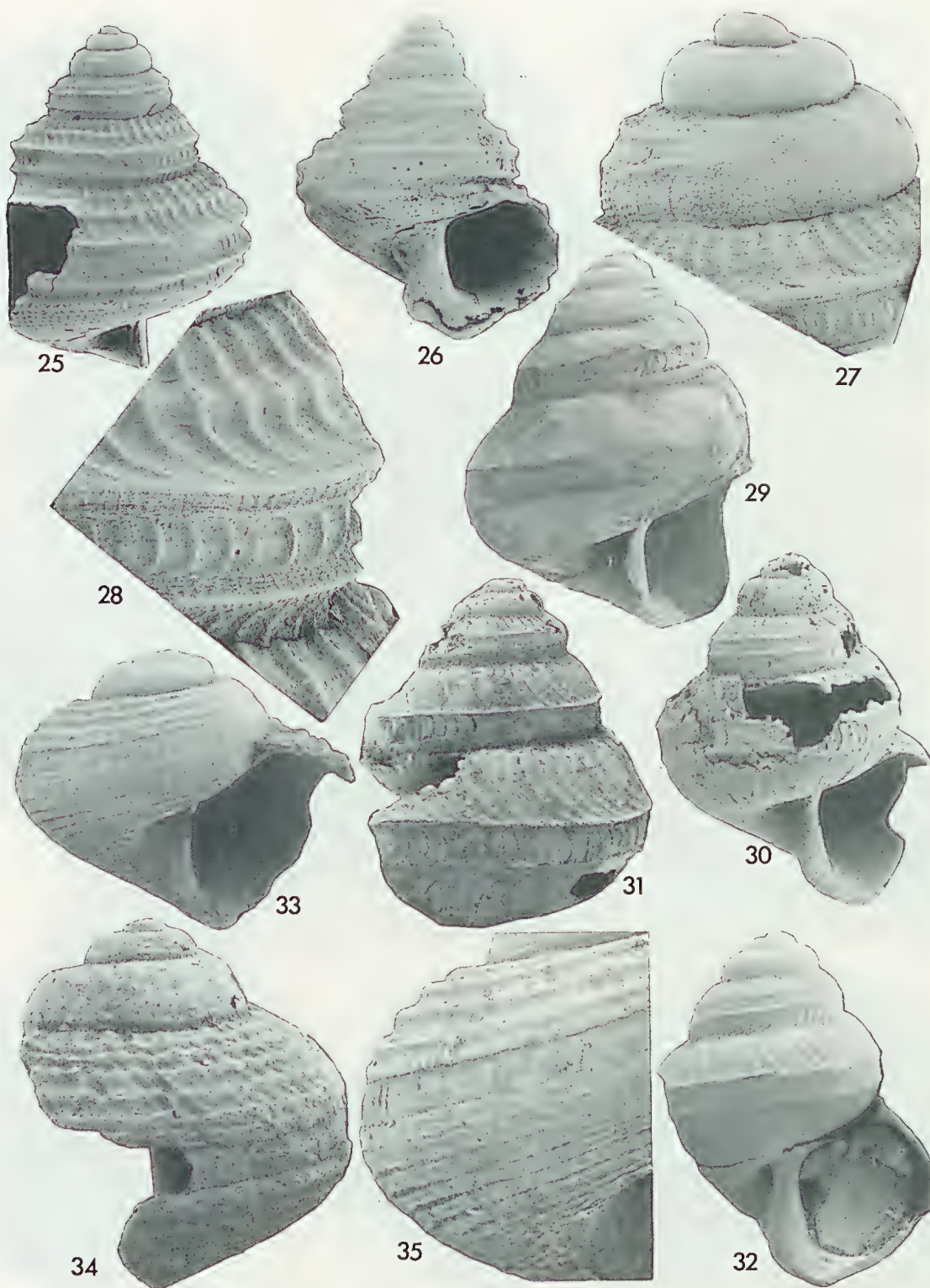
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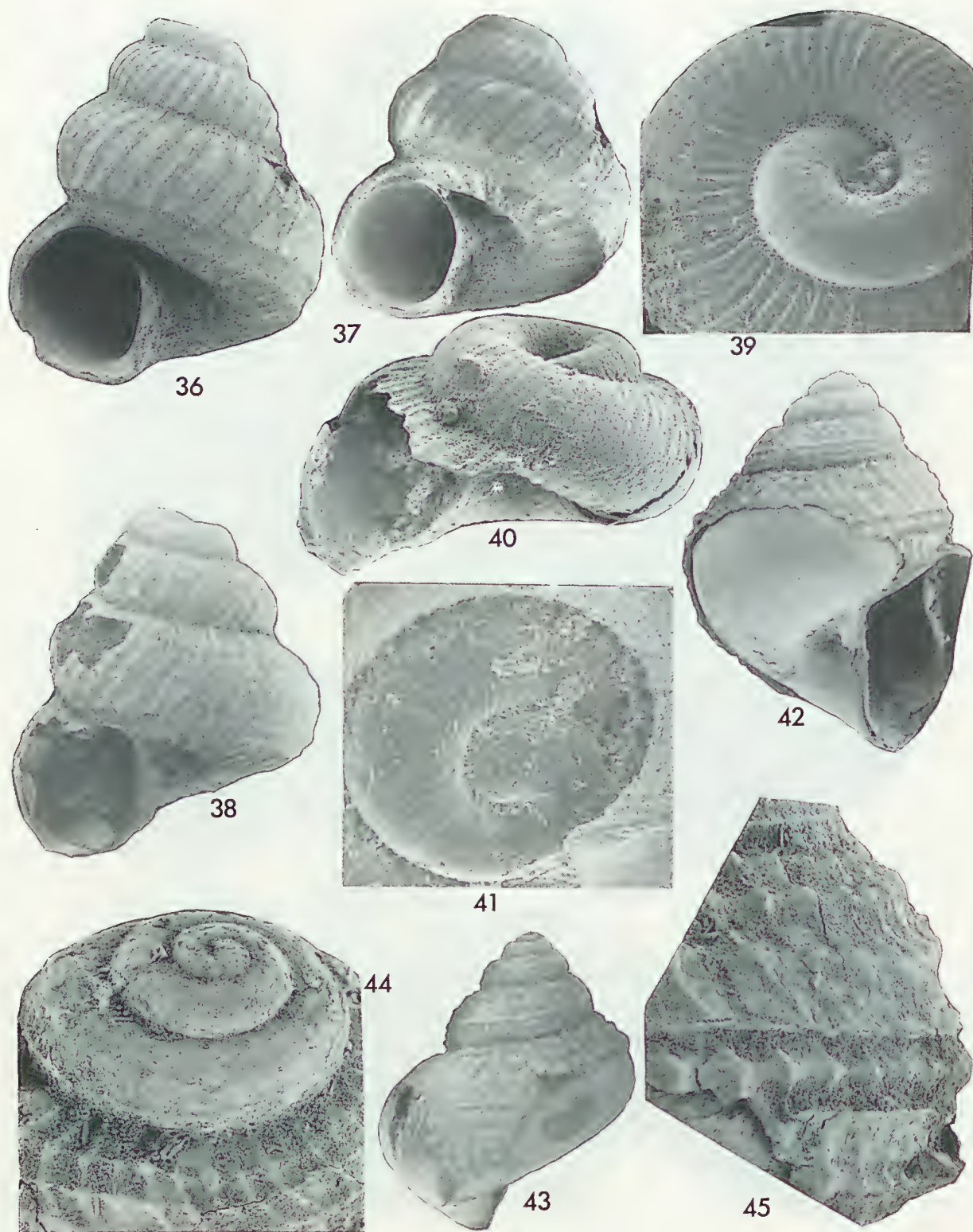
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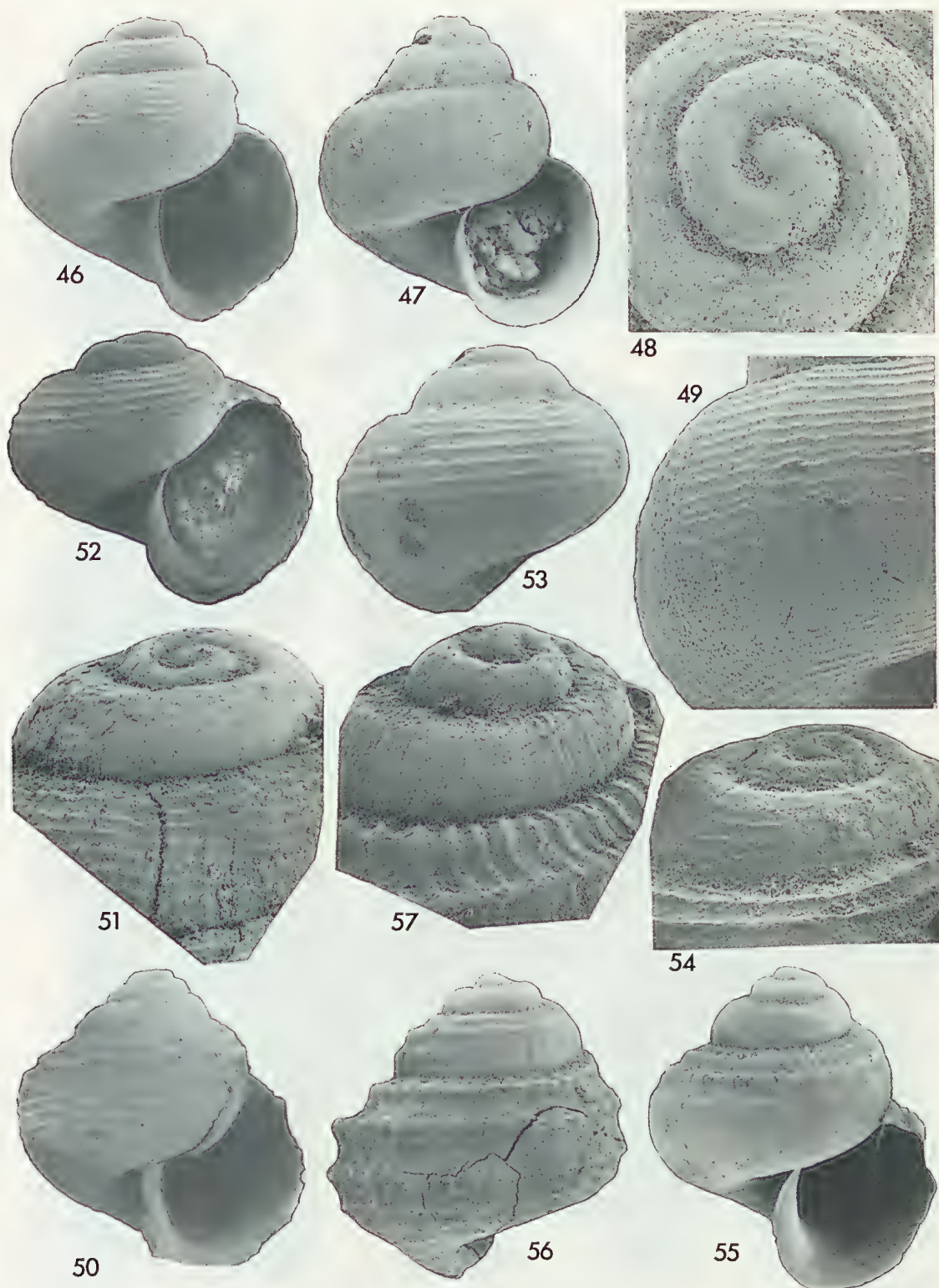
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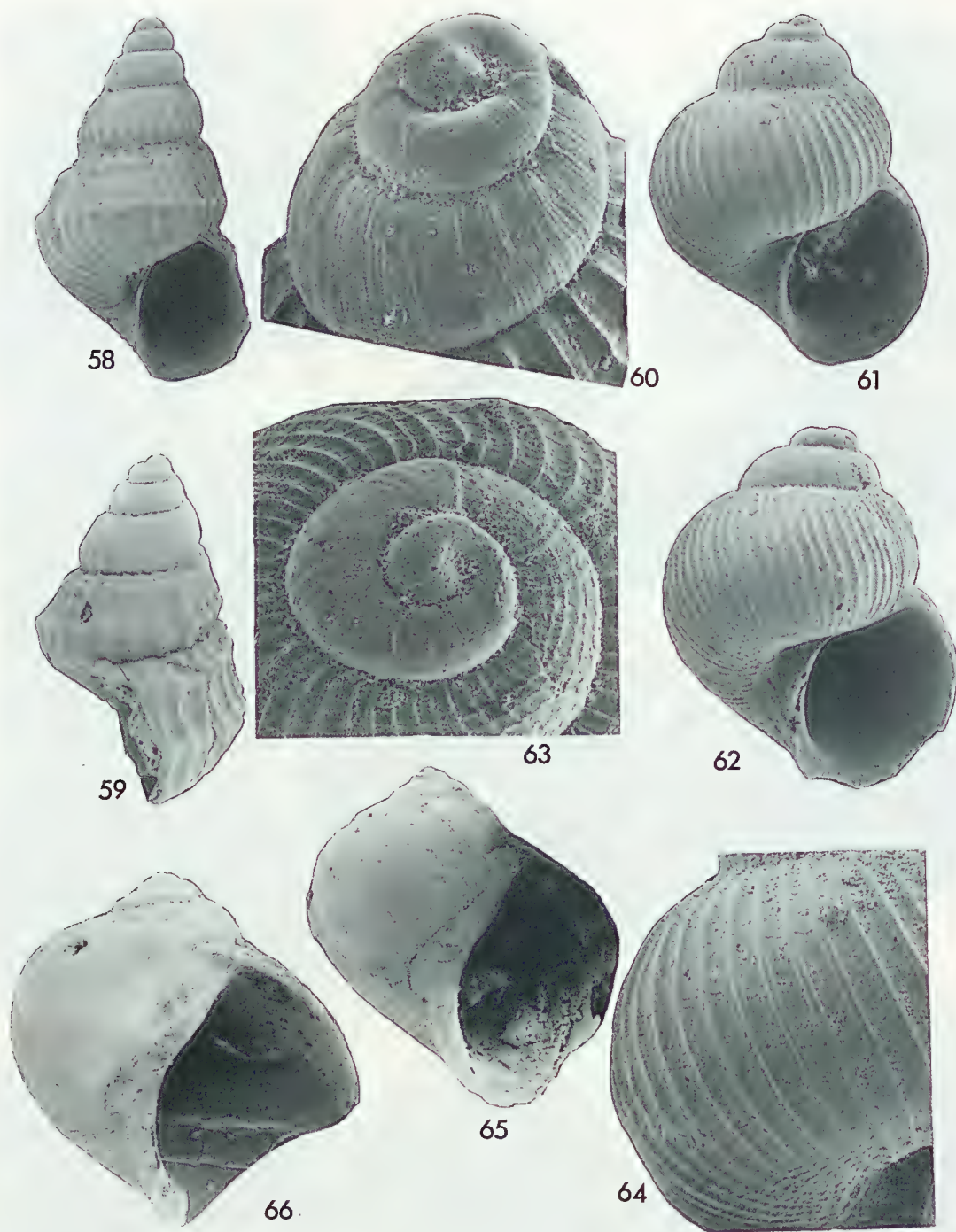
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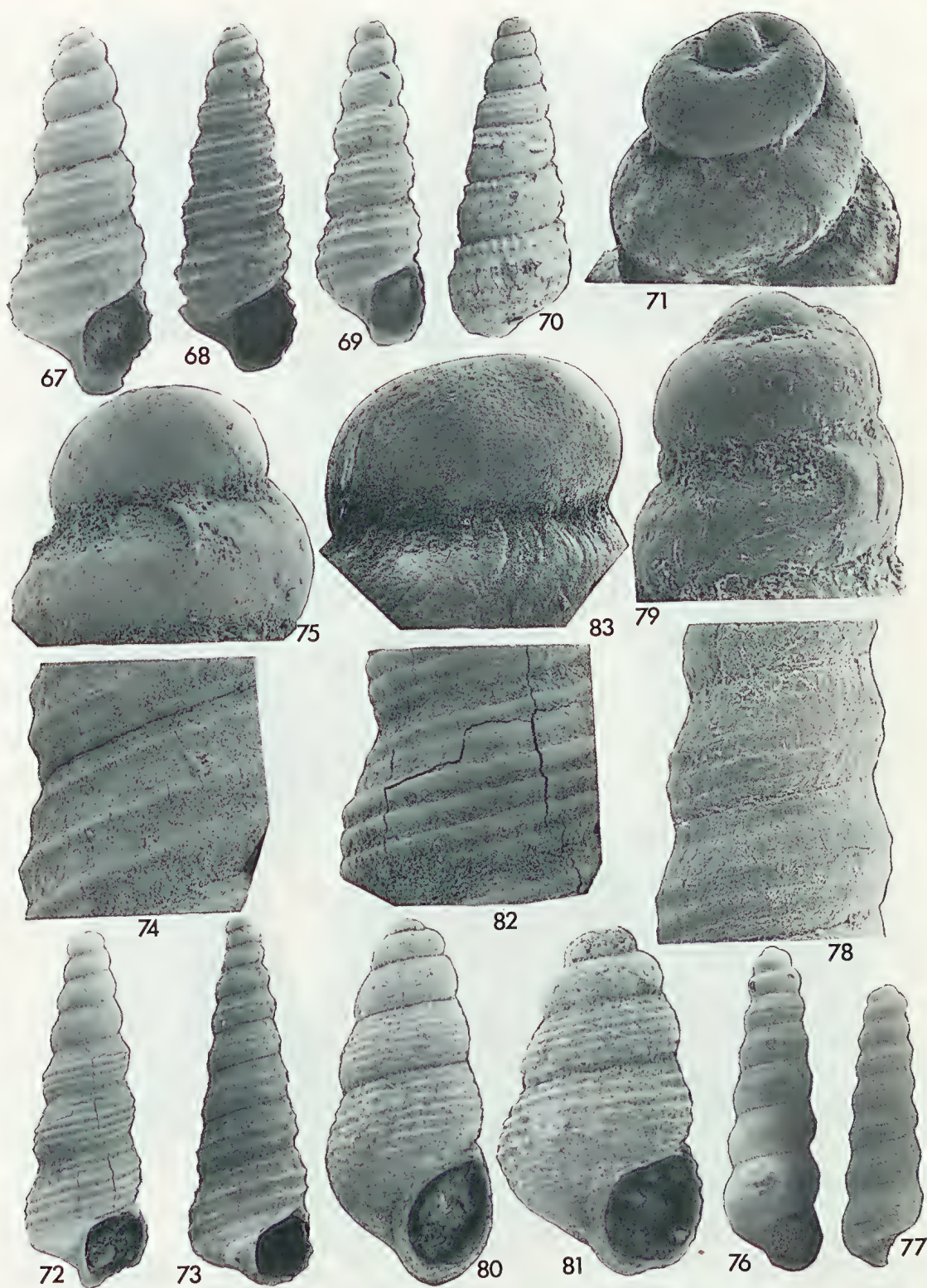
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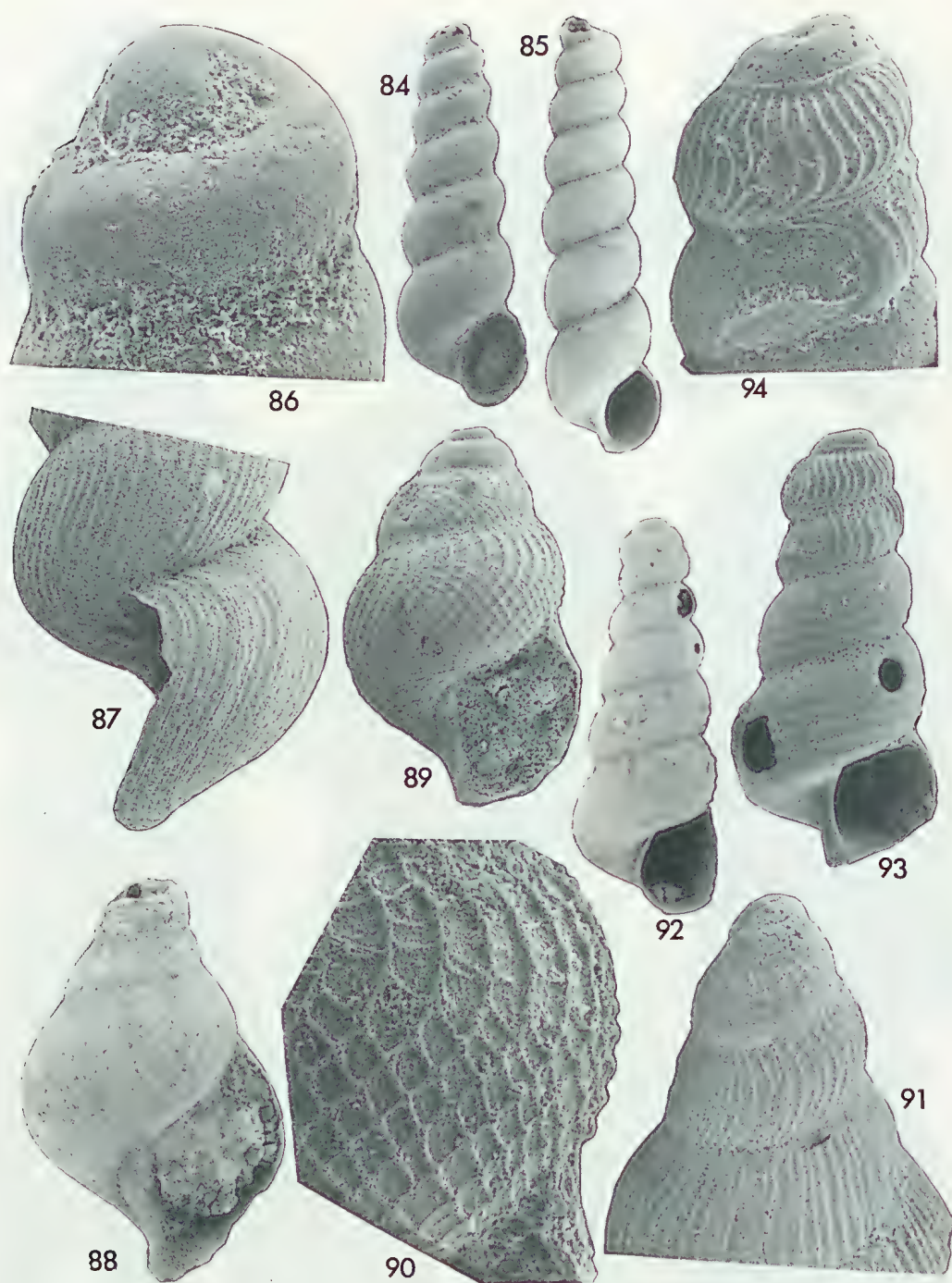
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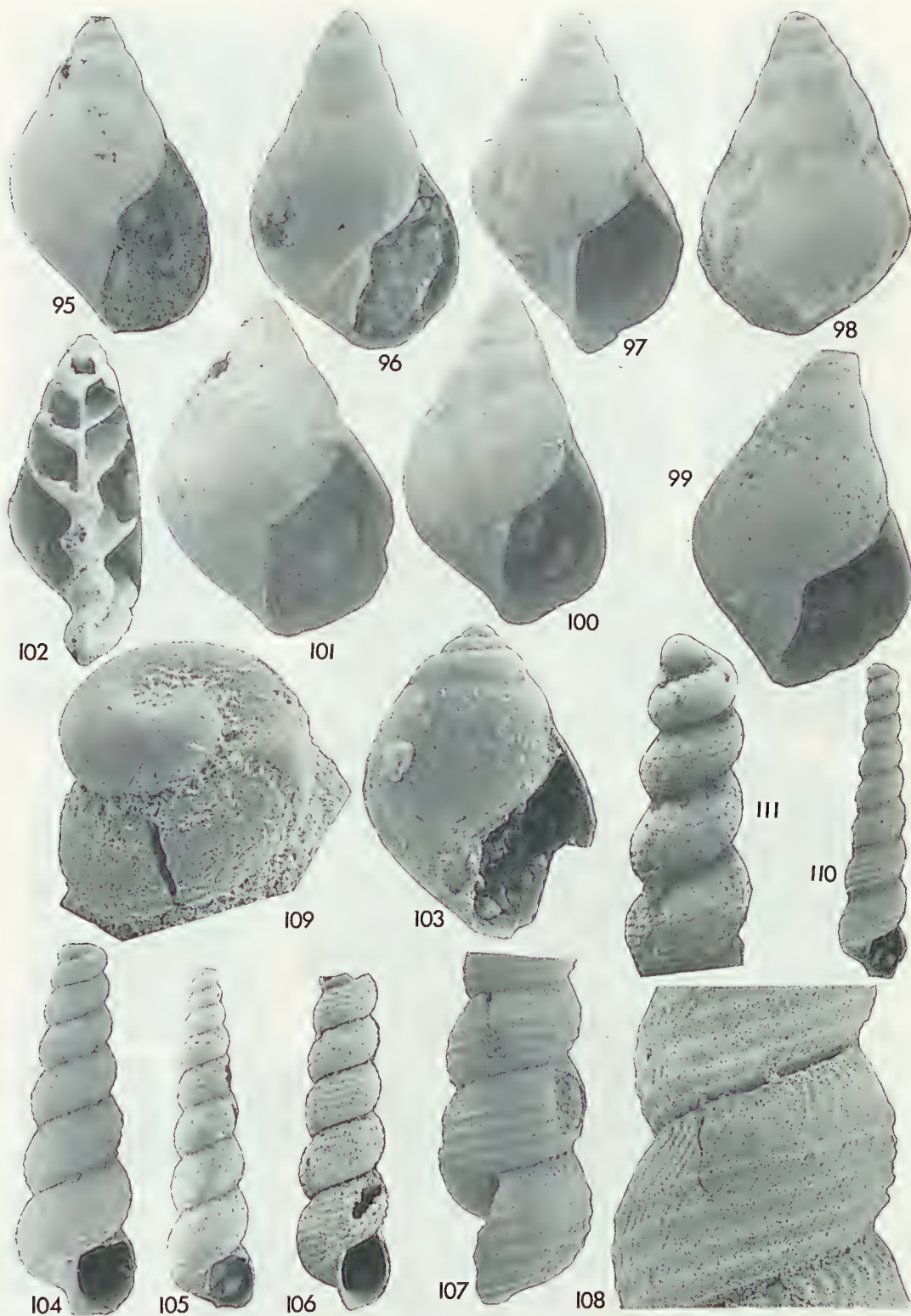
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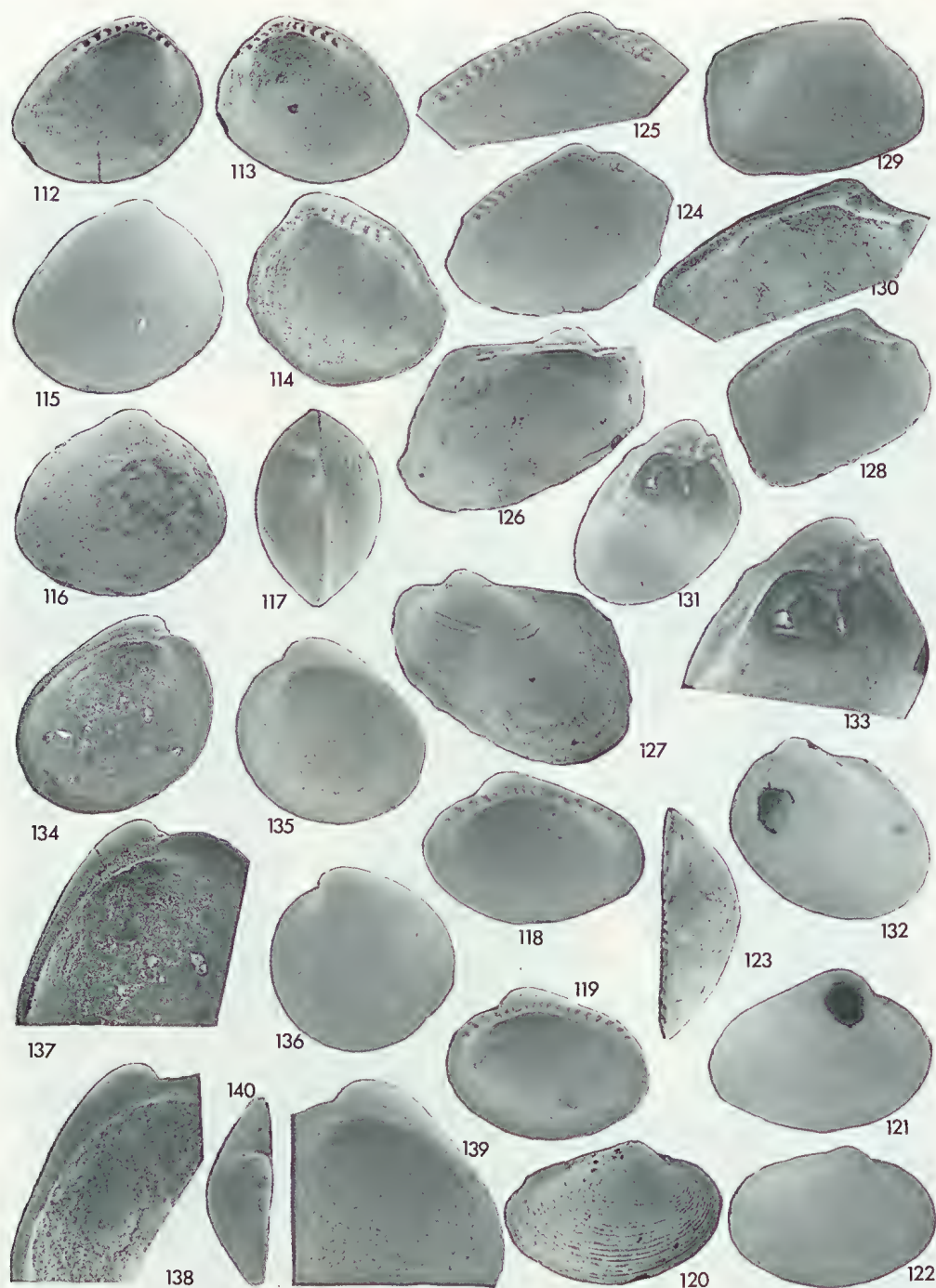
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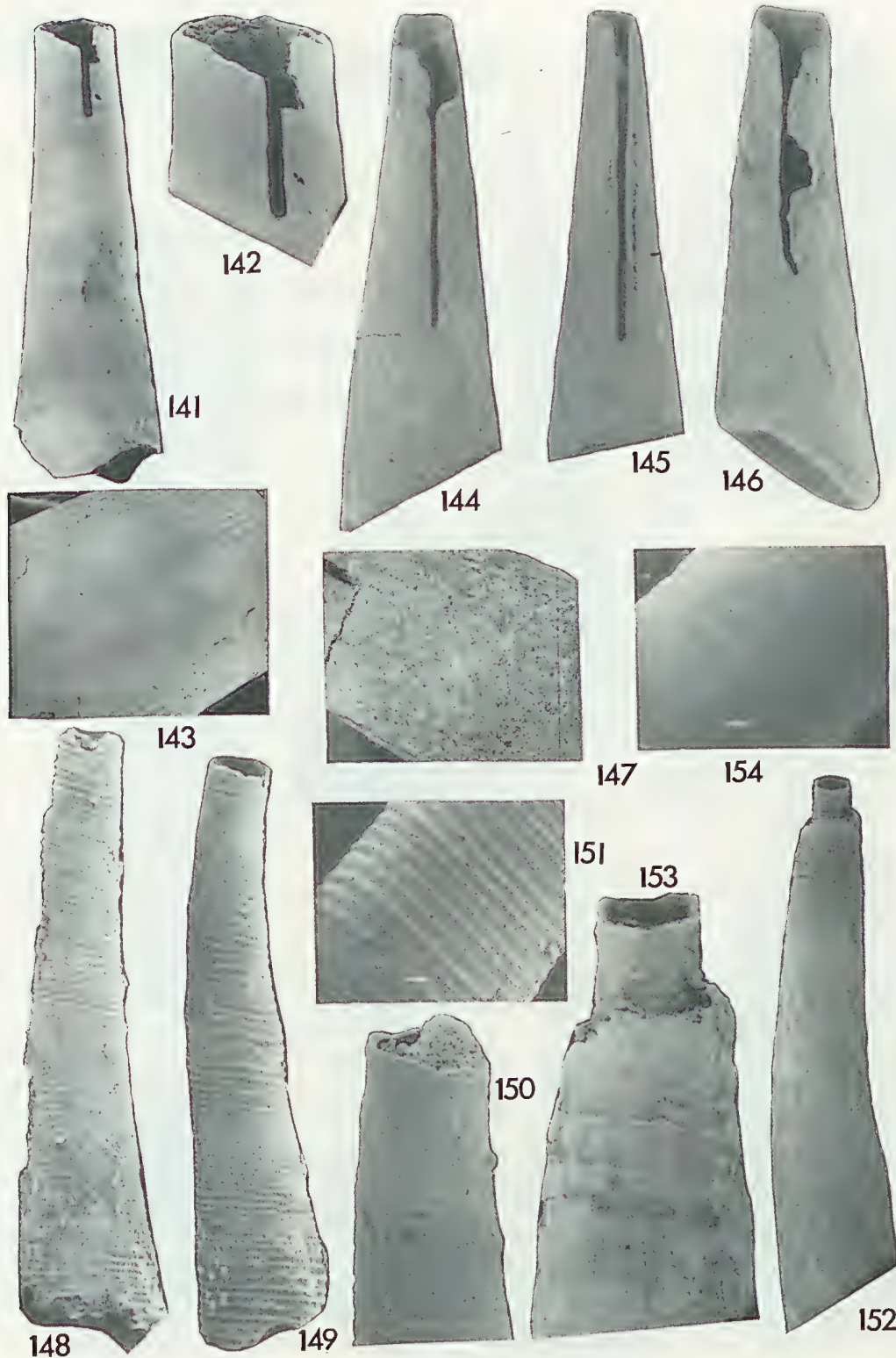
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The genera *Archaeobemlos* n.gen., *Bemlos* Shoemaker, *Protolembos* Myers and *Globosolembos* Myers (Amphipoda, Aoridae, Aorinae) from Australia

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ABSTRACT. Twenty-six species of Aorinae are recorded from Australia of which 21 species are as yet unknown from outside the continent. Sixteen species are new to science and are described and figured. Five further species which were poorly known, which showed minor differences from previously described material, or which were previously unknown from the western Pacific, are also figured. A new genus is erected for *Autonoe philacantha* Stebbing.

MYERS, A.A., 1988. The genera *Archaeobemlos* n.gen., *Bemlos* Shoemaker, *Protolembos* Myers and *Globosolembos* Myers (Amphipoda, Aoridae, Aorinae) from Australia. Records of the Australian Museum 40 (5): 265-332

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Twenty-six species and four genera of Aorinae (*sensu* Myers 1988) are recorded from Australia. Twenty-one species, of which 16 are new to science, are figured. A new genus is erected for *Autonoe philacantha* Stebbing. Previous to the present work, only four species of *Lembos sensu lato* (*Bemlos*

australis (Haswell), *Archaeobemlos philacanthus* (Stebbing), *Protolembos chiltoni* (Myers) and *Globosolembos excavatus* (Myers) were known from Australia. Sampling of the Australian amphipod fauna has as yet been too scanty to allow a satisfactory biogeographic analysis to be performed.

Table 1. Distribution of Australian species of *Bemlos*, *Archaeobemlos*, *Globosolembos* and *Protolembos*. Parentheses indicate deep water occurrence in tropical thermal regime.

	Qld	NSW	Vic.	Tas.	S.A.	W.A.
Tropical Eastern Flock						
<i>Bemlos mollis</i>	+					
<i>Bemlos saloteae</i>	+					
<i>Bemlos tridentatus</i>	+					
<i>Bemlos triangulum</i>	+					
<i>Bemlos bidens</i>	+					
<i>Globosolembos ruffoi</i>	+					
<i>Globosolembos excavatus</i>	+					
<i>Bemlos ephippium ephippium</i>	+	+				
<i>Bemlos australis</i>	+	+				
<i>Bemlos aequimanus</i>	+	+	+			
Cool-warm temperate Southern Flock						
<i>Archaeobemlos philacanthus</i>	(+)		+			
<i>Protolembos murrarum</i>		+				
<i>Bemlos tridis</i>		+				+
<i>Bemlos tris</i>			+			
<i>Bemlos dolichomanus</i>			+			
<i>Bemlos gilgi</i>			+			
<i>Protolembos drummondiae</i>			+			
<i>Protolembos arinyas</i>			+			
<i>Globosolembos lunatus</i>			+			
<i>Protolembos chiltoni</i>			+	+		
<i>Protolembos clematis</i>				+		
<i>Protolembos verrucularum</i>				+		
<i>Bemlos arkoolus</i>			+		+	
Tropical Western Flock						
<i>Bemlos strigilis</i>					+	+
<i>Bemlos quadrimanus</i>						+
<i>Protolembos yaranus</i>						+
<i>Bemlos ephippium disjuncta</i>						+

There appear, however, to be three main flocks (Table 1): 1. tropical eastern Australia, 2. cool-warm temperate southern Australia, and 3. tropical western Australia. The cool-warm temperate element interdigitates with the tropical elements on eastern and western coasts. Only one species, *Bemlos ephippium* n.sp. is known from both eastern and western coasts (as different subspecies), but *Protolembos arinyas* n.sp. and *P. yaranus* n.sp. form a sibling pair, the former from Victoria, the latter from Western Australia.

Of the four genera discussed here, *Archaeobemlos* n.gen. and *Protolembos* are with one exception, unique to Australia and are cool-warm temperate

taxa (the exception being *Protolembos kidoli* from East Africa), while *Bemlos* and *Globosolembos* are primarily tropical. Of the five species in the present work which have extrinsic distributions, one (*Bemlos quadrimanus*) is western Australian and has a broad Indian Ocean distribution westward to East Africa, and four are eastern Australian. Of these, two (*Bemlos aequimanus* and *B. saloteae*) have west Pacific distributions and two (*Globosolembos excavatus* and *G. ruffoi*) have Indian Ocean distributions, although the former extends eastwards to Tonga.

Keys to Australian taxa are provided, but females and juveniles cannot readily be identified.

Key to the Aorinae of Australia

1. Mandible palp article 2 longer than 3 *Archaeobemlos*
 —Mandible palp article 3 longer than 2 2
2. Uropod 1 peduncle shortened, only a little longer than broad, inter-ramal process much longer than peduncle and over two thirds length of rami
 *Australomicrodeutopus*
 —Uropod 1 peduncle not markedly shortened, much longer than broad, inter-ramal process shorter than peduncle and less than two thirds length of rami 3

3. Maxilliped basis with strong flange on anterior margin *Protolembos*
 —Maxilliped basis lacking flange 4
4. Male gnathopod 1 merus greatly elongated extending over much of length or
 exceeding length of elongate carpus *Aora*
 —Male gnathopod 1 merus not greatly elongated, never exceeding length of
 carpus 5
5. Gnathopod 1 greatly enlarged in both sexes, propodus lacking an intrapalmar
 sinus or strong tooth 6
 —Gnathopod 1 greatly enlarged in males only, propodus generally with
 intrapalmar sinus and strong tooth *Bemlos*
6. Gnathopod 2 carpus with strongly setose anterodistal expansion *Xenocheira*
 —Gnathopod 2 carpus lacking setose anterodistal expansion *Globosolembos*

Archaeobemlos n.gen.

Type species. *Autonoe philacantha* Stebbing 1888 (by monotypy).

Diagnosis. Mandible palp article 2 strongly setose, longer than article 3, article 3 falcate, posterior margin strongly setose, setae of varying length, some marginal setae longer than distal setae, left mandible molar with crenulate ridges traversing molar. Maxilla 1 outer plate with 11 terminal spines, palp article 2 broad, with setal row on anterodistal margin. Gnathopod 1 enlarged, similar in both sexes. Pereopods 5 and 6 propodus posterior margin with several spines. Uropod 3 rami with marginal spines inner ramus with marginal setae, both rami with long distal setae outer ramus lacking a second article.

Remarks. In its non sexually dimorphic gnathopoda, this genus resembles the plesiomorphic genus *Arctolembos* Myers, but also the otherwise rather apomorphic *Globosolembos* Myers. It also resembles *Arctolembos* in the mandibular palp shape and setation, but differs in the unmodified head lobes, normal labium, normal maxilliped, ridged molar and much less spinous uropods. It resembles *Protolembos* Myers in the mandibular palp and uropod structure, but that genus has rounded molar plates, maxilliped flanges and sexually dimorphic gnathopoda.

Archaeobemlos philacanthus (Stebbing)

Figs 1–3

Autonoe philacantha Stebbing, 1888: 1082, pl. 110;—
 Stebbing, 1906: 598, fig. 102;—Stebbing, 1910: 605;—
 Sheard, 1937: 26.

Material examined. Victoria: 38 males, 45 females, + 5 slides male, 1 slide female, Bass Strait, 40°09.2'S 147°31.9'E, 51 m, shell gravel, 14 Nov 1981, NZ01 R.V. *Tangaroa* stn 162, AM P37401; Queensland: 5

males, 14 females, north-east of Lady Elliot Island, 24°03.7'S 152°49.4'E, 150 m, rubble bottom with small disc corals, 4 July 1984, HMAS *Kimbla* stn 3, AM P37402.

Description. Body (in alcohol) of a uniform pale tan. Male pereon segments lacking sternal processes. Head anteroventral margin scarcely produced. Labium outer plate distal margin with about 5 spines. Mandible palp article ratios 4 : 12 : 11, article 2 posterior margin setose, article 3 posterior margin concave, strongly setose, the setae of variable length, some marginal setae longer than distal setae; mandible molar with 7 crenulate ridges traversing it. Maxilla 1 outer plate with 11 terminal spines, palp article 1 very short, palp article 2 with setal row on anterodistal margin and with 6 terminal spines. Antenna 1 about two thirds body length, penduncular articles in the length ratios 7 : 8 : 3; accessory flagellum with 5 articles, the terminal article rudimentary; primary flagellum a little longer than peduncle with about 26 articles. Antenna 2 about two thirds length of antenna 1, peduncular articles 4 and 5 subequal; flagellum a little longer than peduncular article 5, with about 10 articles. Gnathopod 1 (both sexes) coxa subquadrangular, anterodistal margin rounded; basis robust about one and one half times as long as broad; carpus almost as broad as long; propodus longer than carpus, palm long, oblique and sinuous, defined by a triangular tooth and a spine; dactylus fitting palm. Gnathopod 2 (both sexes) basis stout; propodus longer than carpus, palm oblique, defined by a weak hump and a spine; dactylus fitting palm. Pereopods 3 and 4 dactylus little over half length of propodus. Pereopods 5–7 in the length ratios 2 : 3 : 4; pereopod 7 about three quarters body length. Epimera 1–3 rounded. Uropod 1 peduncle with inter-ramal tooth one quarter length of peduncle; rami slender, spinose, inner ramus slightly the longer, but shorter

than peduncle. Uropod 2 lacking interramal process; rami stout, spinose, inner ramus a little longer than outer and longer than peduncle. Uropod 3 inner ramus distinctly longer than outer and nearly twice length of peduncle; both rami with marginal spines and long terminal setae; inner ramus with marginal setae.

Habitat. On gravel, sand and mud bottoms in depths of 50–150 m.

Distribution. Probably widely distributed on suitable bottoms from Victoria to Queensland.

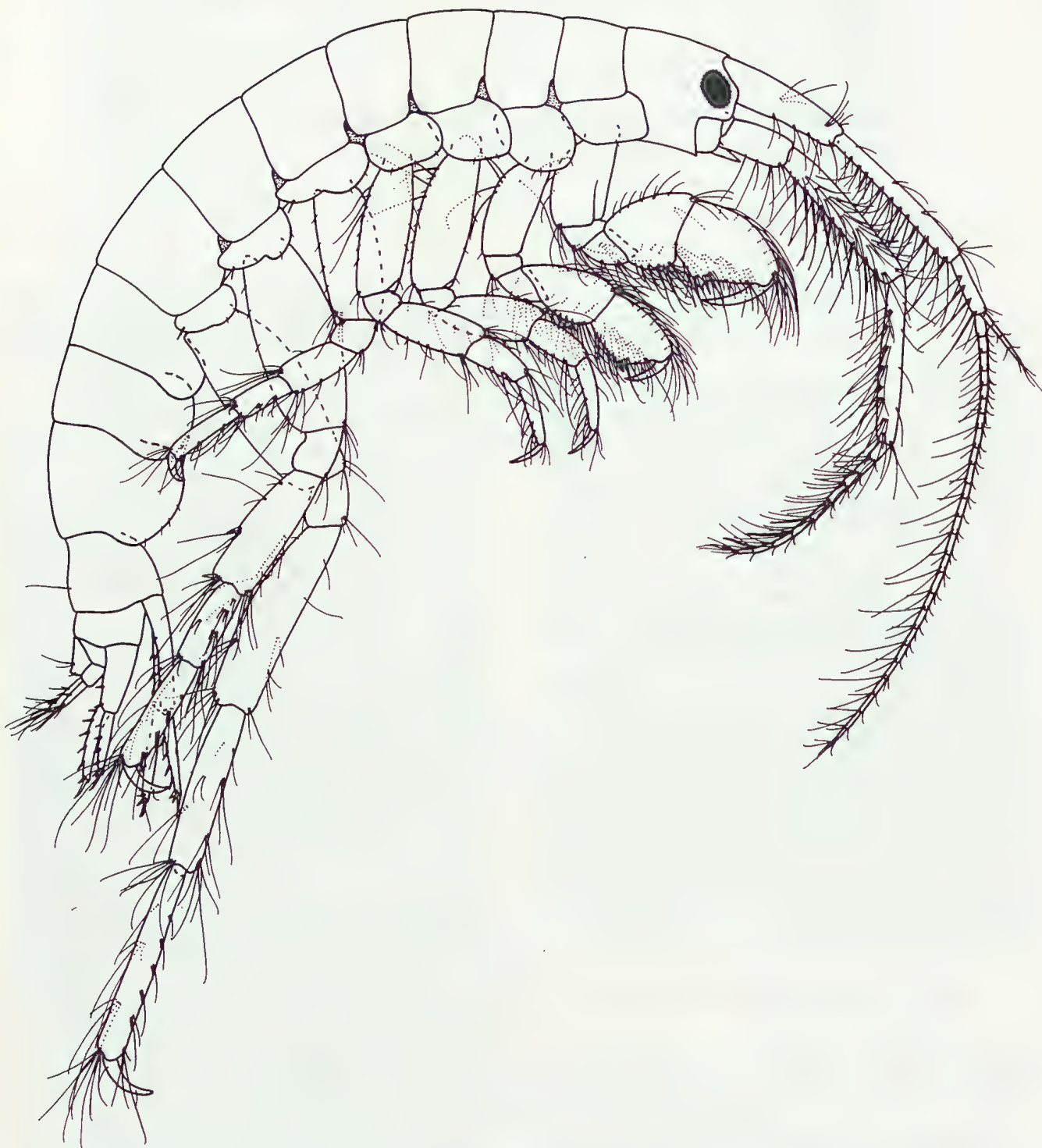


Fig.1. *Archaeobemlos philacanthus* (Stebbing), male, 10.0 mm, Bass Strait.

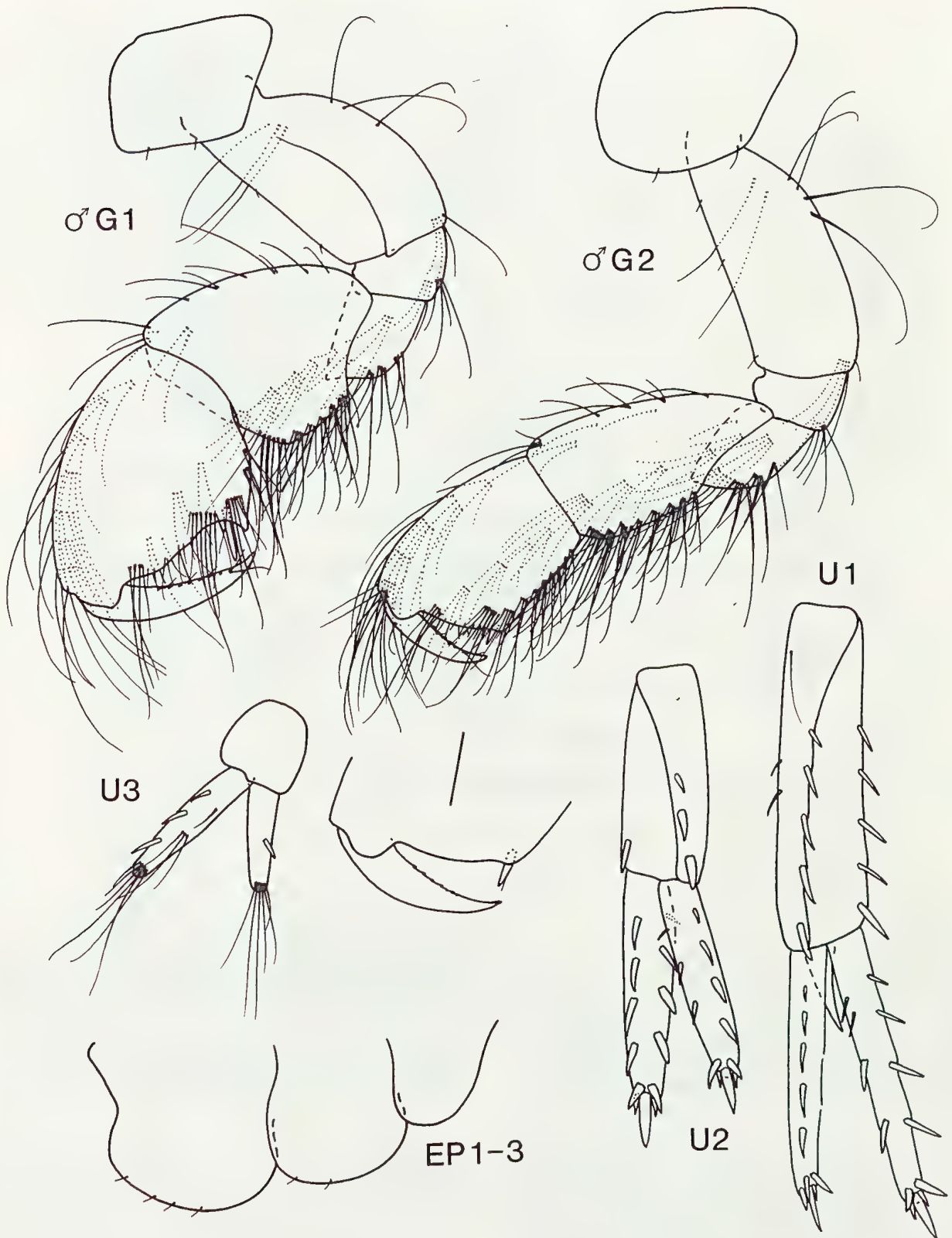


Fig.2. *Archaeobemlos philacanthus* (Stebbing), male, 10.0 mm, Bass Strait.

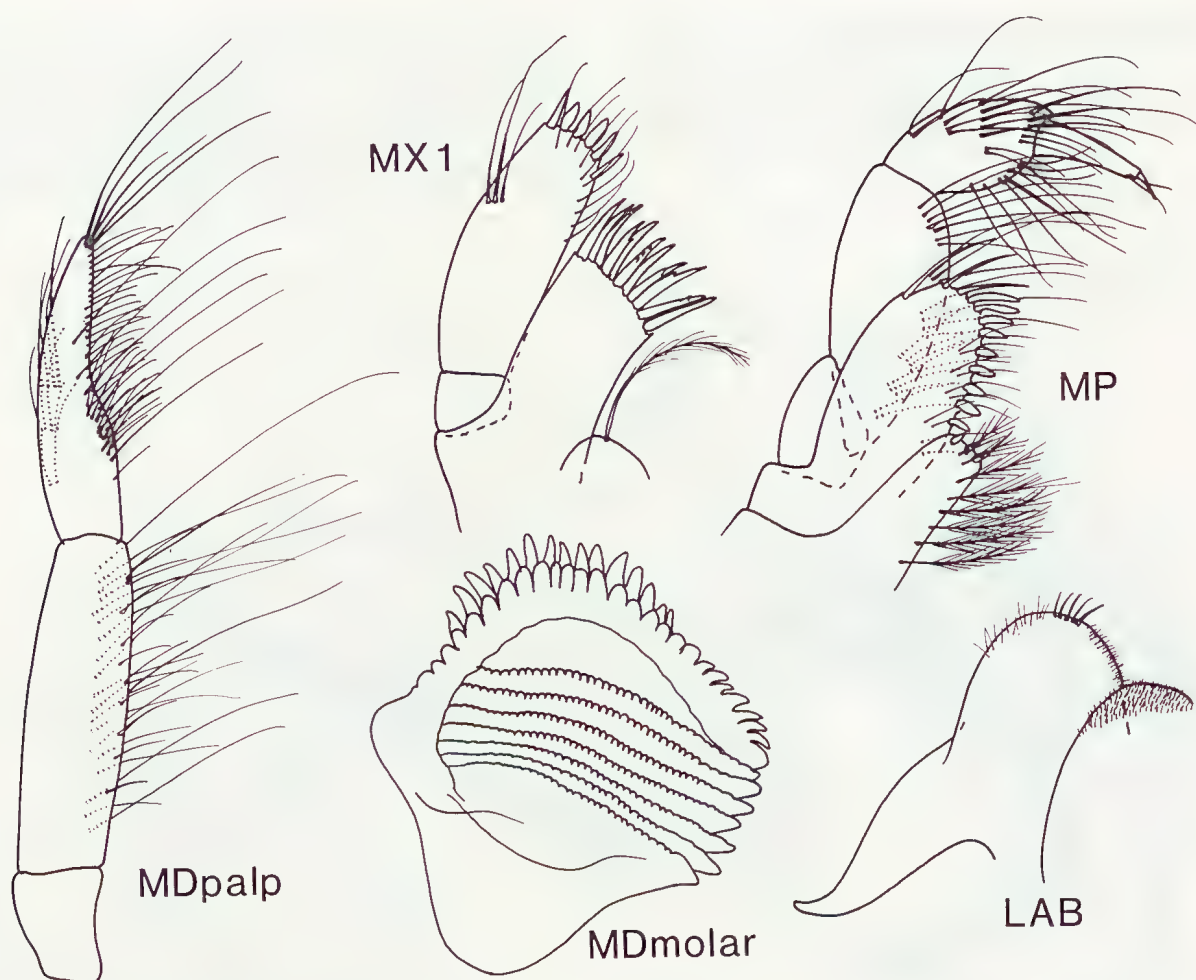


Fig.3. *Archaeobemlos philacanthus* (Stebbing), male, 10.0 mm, Bass Strait.

Bemlos Shoemaker

Bemlos Shoemaker, 1925: 36; Myers, 1988: 188.

Type species. *Bemlos macromanus* Shoemaker.

Diagnosis. Mandible palp article 2 usually less than two thirds length of article 3, weakly setiferous, article 3 generally not markedly falcate, posterior margin with setae of 2 distinct lengths, left molar with well-developed plates, rounded or with primary

plate falcate. Maxilla 1 outer plate with 10 spines. Maxilliped without flanges. Male pereon generally with sternal processes. Gnathopod 1 always sexually dimorphic. Gnathopod 2 of similar size in both sexes but sometimes sexually dimorphic. Pereopods 5 and 6 propodus posterior margin with several spines. Uropod 3 rami weakly spinous with very long terminal setae outer ramus with small second article.

Key to male *Bemlos* of Australia

1. Gnathopod 1 carpus larger than propodus 2
 —Gnathopod 1 carpus smaller than propodus 4
2. Gnathopod 1 carpus lacking teeth 3
 —Gnathopod 1 carpus posterior margin with stout teeth *B. tridentatus*
3. Pereon segments 2–3 with strong acute sternal processes *B. triangulum*
 —Pereon segments lacking sternal processes *B. australis*

4. Gnathopod 2 carpus anterior margin densely setose 5
- Gnathopod 2 carpus anterior margin weakly setiferous 6
5. Gnathopod 1 basis with wing-like process on outer face (Fig. 37) lacking posterodistal brush of long setae *B. arkoolus*
- Gnathopod 1 basis lacking wing-like process on outer face, with posterodistal brush of long setae *B. mollis*
6. Pereon segments 1–7 or 2–7 with dense brown bands or blocks of pigment (Fig. 10) *B. ephippium*
- Pereon segments not pigmented as above 7
7. Gnathopod 1 merus and carpus each with posterodistal tooth 8
- Gnathopod 1 merus and carpus lacking teeth 9
8. Gnathopod 2 basis very elongate and slender (Fig. 37) *B. tris*
- Gnathopod 2 basis not markedly elongate and slender (Fig. 25) *B. bidens*
9. Gnathopod 2 basis anterodistal corner produced into a distinct tooth 10
- Gnathopod 2 basis anterodistal corner not produced into a tooth 13
10. Gnathopod 1 propodus broad, less than one and one half times as long as broad *B. quadrimanus*
- Gnathopod 1 propodus slender, more than one and one half times as long as broad 11
11. Gnathopod 1 dactylus less than half length of propodus, scarcely overlapping palmar defining tooth *B. dolichomanus*
- Gnathopod 1 dactylus over half length of propodus, greatly overlapping palmar defining tooth 12
12. Gnathopod 1 palm terminating acutely, pereon processes acute *B. saloteae*
- Gnathopod 1 palm terminating obtusely, pereon processes obtuse *B. aequimanus*
13. Gnathopod 1 propodus much broader distally, basis and carpus with stridulating ridges *B. strigilis*
- Gnathopod 1 propodus not broader distally, basis and carpus lacking stridulating ridges 14
14. Gnathopod 1 propodus with strong posterodistal tooth *B. trudis*
- Gnathopod 1 propodus lacking posterodistal tooth *B. gilgi*

***Bemlos mollis* n.sp.**

Figs 4–6

Type material. HOLOTYPE: male, 3.0 mm. Lizard Island, Qld, rubble and algal turf on top of patch reef in lagoon 1.5 m, 15 Jan 1982, coll. B. Kensley, AM P37403. PARATYPES: 1 female, + slide, type locality, AM P37404. PARATYPE: 1 male, + 4 slides, reef off North Point, rubble and *Amphiroa* from reef crest 3 m, 12 Jan 1982, B. Kensley, AM P37406.

Additional material. Lizard Island, Queensland: 2 males, 2 females, between South Island and Bird Island, scattered coral heads, rubble from depressions in coral, 7.7–9.0 m, 9 Jan 1982, B. Kensley, AM P37405.

Description. Body (in alcohol) white, with weak, irregular, narrow dorsal bands of reddish brown

pigment on pereon segments 2 and 5–7. Male pereon segment 2 with slender, acute, midventral sternal process, pereon segments 3–4 with short, subacute sternal processes. Head anteroventral margin quite strongly produced but subacute. Labium outer plate distal margin with about 8 spines. Mandible palp article ratios 4 : 9 : 13, article 3 posterior margin straight and setiferous over two thirds of its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 6 distal spines. Antenna 1 very slender, slightly exceeding body length, peduncular articles in the length ratios 5 : 8 : 3; accessory flagellum with 4 articles, the terminal article rudimentary; primary flagellum about one and one half times length of

peduncle with up to 15 articles. Antenna 2 very slender, two thirds length of antenna 1, peduncular articles 4 and 5 subequal; flagellum a little shorter than peduncular article 5 with about 8 articles. Male gnathopod 1 coxa subquadrangular, anterodistal margin rounded; basis swollen mediodistally, anterior margin weakly convex, posterior margin strongly convex bearing a distal brush of very long setae; carpus well developed, a little longer than broad, with a small, triangular, posterodistal tooth; propodus less than twice as long as carpus, broadening distally, palm straight in anterior portion, with relatively deep, narrow, triangular excavation in posterior portion, defining tooth slender, acute, with proximal spine; dactylus

elongate, overlapping palm. Female gnathopod 1 slender, basis over 3 times as long as broad; propodus a little longer than carpus, broadening distally, palm very slightly sinuous; dactylus overlapping palm. Male gnathopod 2 basis anterior margin very weakly concave, posterior margin strongly convex; merus posterior margin with numerous long setae; carpus distinctly longer than propodus; carpus and propodus anterior margins strongly setose; dactylus fitting palm. Female gnathopod 2 slender, basis over 4 times as long as broad; carpus and propodus subequal in length; propodus widening distally; dactylus fitting palm. Pereopods 3 and 4 dactylus two thirds length of propodus. Pereopods 5-7 delicate and slender, in the length ratios 2 : 3 : 5; pereopod 7



Fig.4. *Bemlos mollis* n.sp., male, 3.0 mm, Lizard Island.

almost equal to body length. Epimera 1-3 rounded. Uropod 1 peduncle with inter-ramal tooth less than one third length of peduncle; rami slender, outer ramus a little longer than inner and longer than peduncle. Uropod 2 peduncle with inter-ramal tooth a little less than half length of peduncle; outer ramus longer than inner and one and one half times length of peduncle. Uropod 3 rami elongate; inner ramus longer than outer, and two and one half times length

of peduncle; outer ramus with small second article; both rami with very long terminal setae which exceed length of rami.

Remarks. The extremely elongate and slender antennae and pereopods of this species readily distinguish it from all other Australian species.

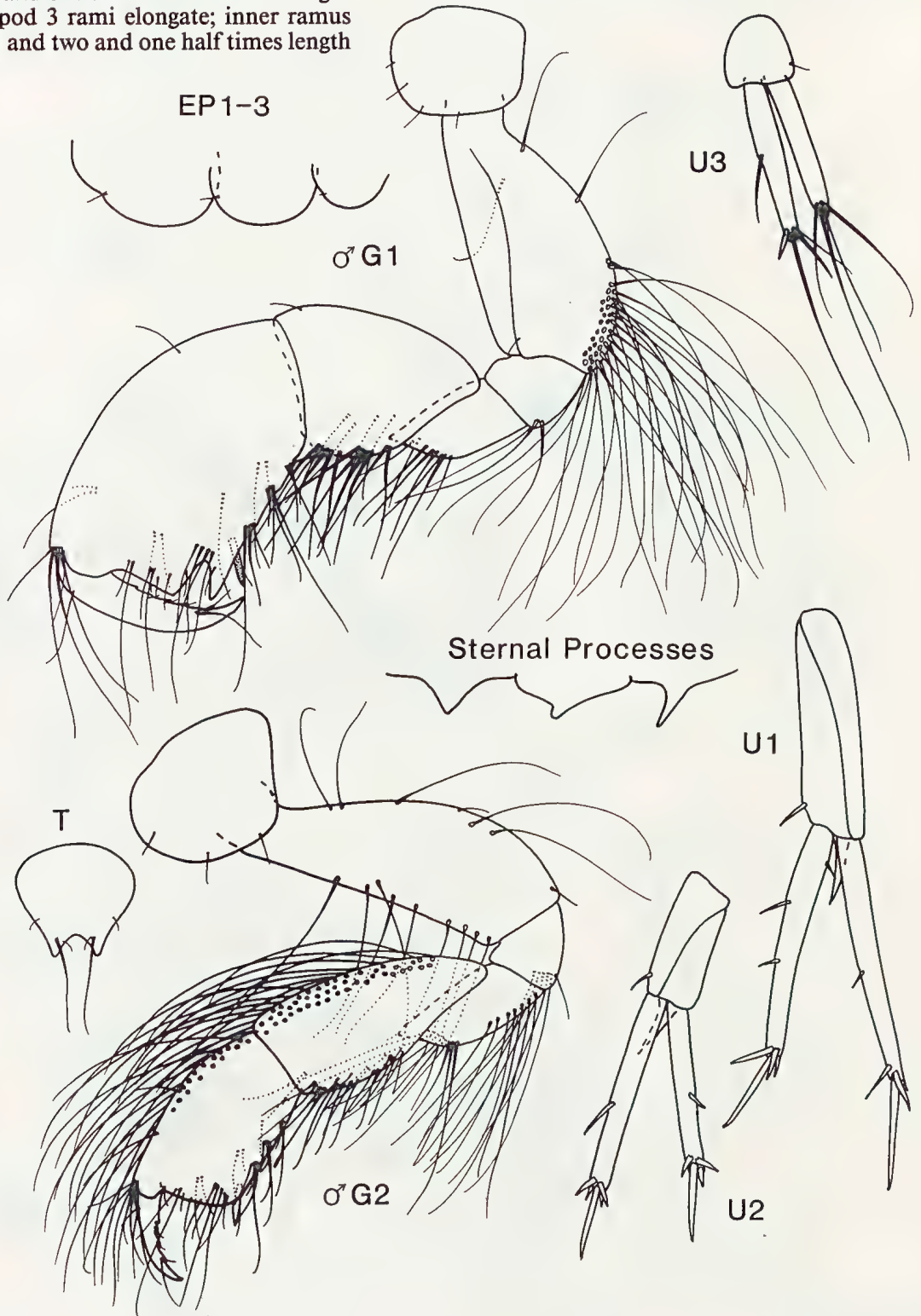


Fig.5. *Bemlos mollis* n.sp., male, 3.0 mm, Lizard Island.

Habitat. Among algal turf and reef rubble.

Distribution. At present known only from Lizard Island, Queensland.

Etymology. From the latin *mollis* = pliant, referring to its slender appendages.

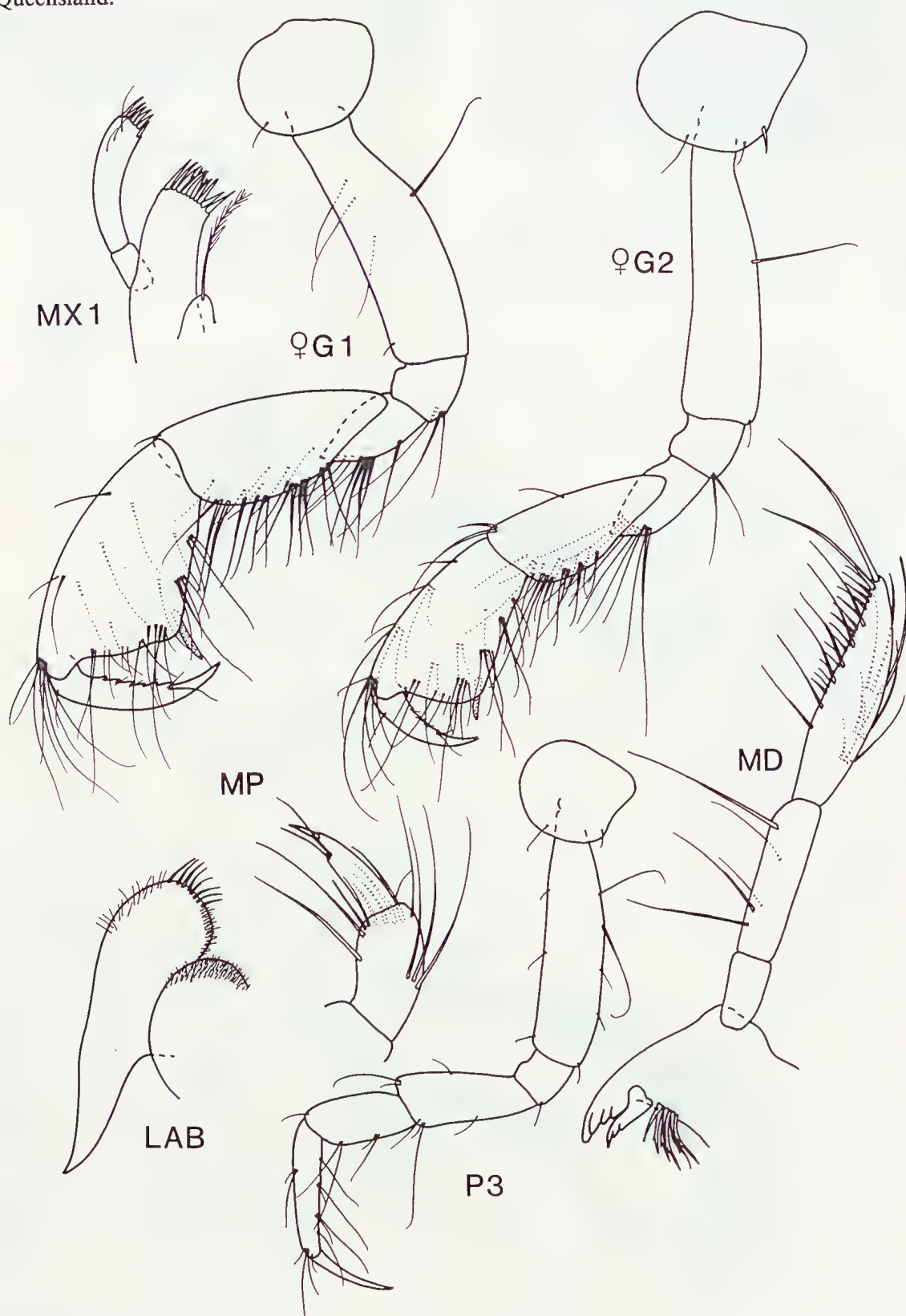


Fig.6. *Bemlos mollis* n.sp., male, female, 3.0 mm, Lizard Island.

***Bemlos ehippium* n.sp.**

Figs 7-10

Type material. HOLOTYPE: male, 2.8 mm. Lizard Island, Queensland, rubble from depressions in crest of patch reef in lagoon, 1.5-2.5 m, 16 Jan 1982, B. Kensley, AM P37407. PARATYPES: 2 females, + 1 slide, type locality, AM

P37408. PARATYPE: 1 male, + 4 slides. Lizard Island, Qld, reef flat between Bird Island and South Island, algal encrusted rubble, 1.5-2.5 m, 16 Jan 1982, B. Kensley, AM P37409.

Additional material. Lizard Island, Queensland: 1 female, between South Island and Palfrey Island, algal turf from shallow ridge between islands, 1.0-1.5 m, 14 Jan

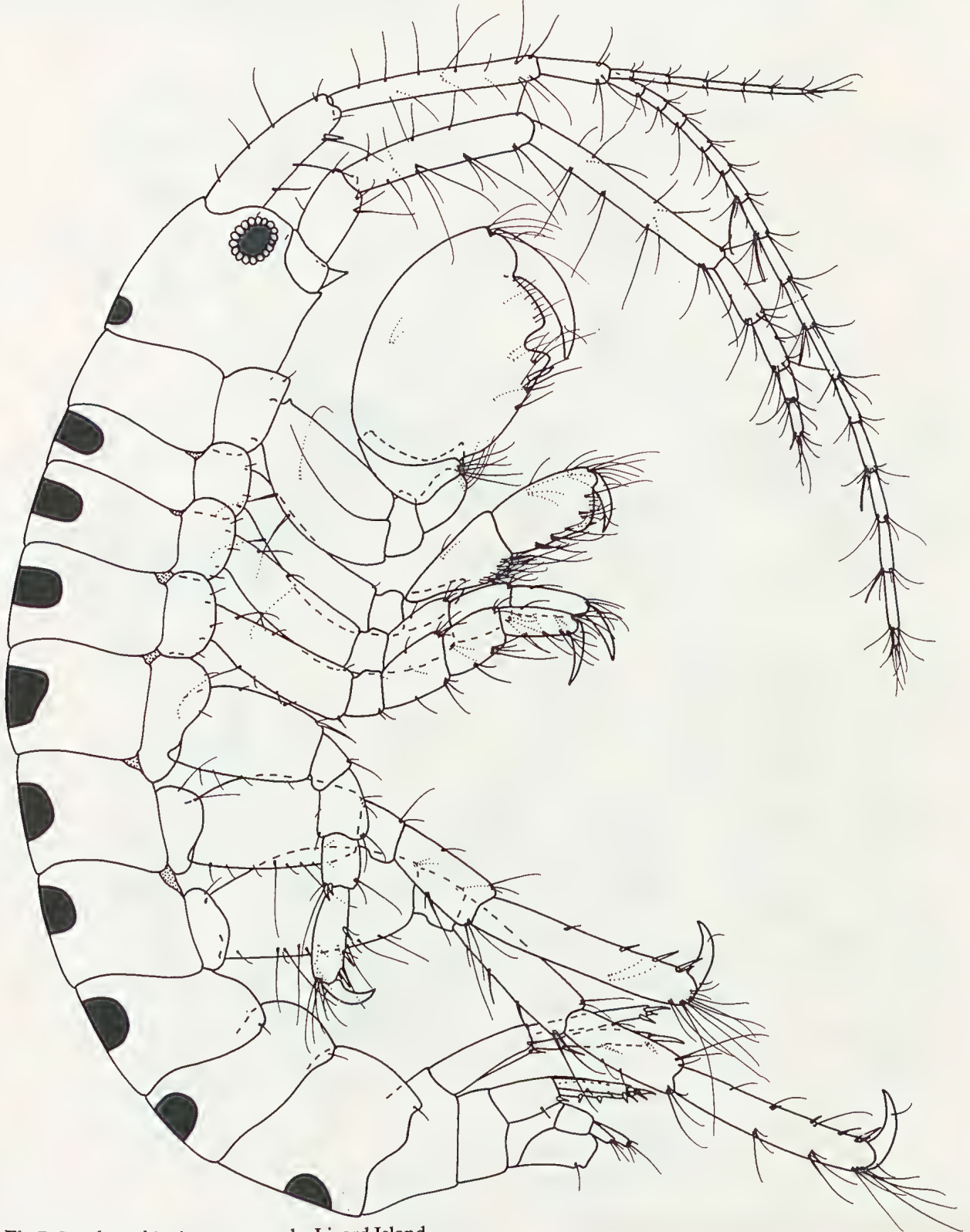


Fig.7. *Bemlos ehippium* n.sp., male, Lizard Island.

1982, B. Kensley, AM P37410. New South Wales: 3 males, Broom Heads in *Ecklonia radiata* holdfasts, 0.5 m, 5 Sept 1986, A.A. Myers, AM P37411; 1 male, 2 females, Broom Heads, in *Sargassum* sp., 0.5 m, 5 Sept 1986, A.A. Myers,

AM P37412; 1 male, 3 females, Byron Bay, in *Sargassum*, 0.5 m, 6 Sept 1986, A.A. Myers, AM P37413; 1 female, Woolgoolga, in *Jania*, islet connected to mainland at L.T., 0.25 m, 3 Sept 1986, A.A. Myers, AM P37414.

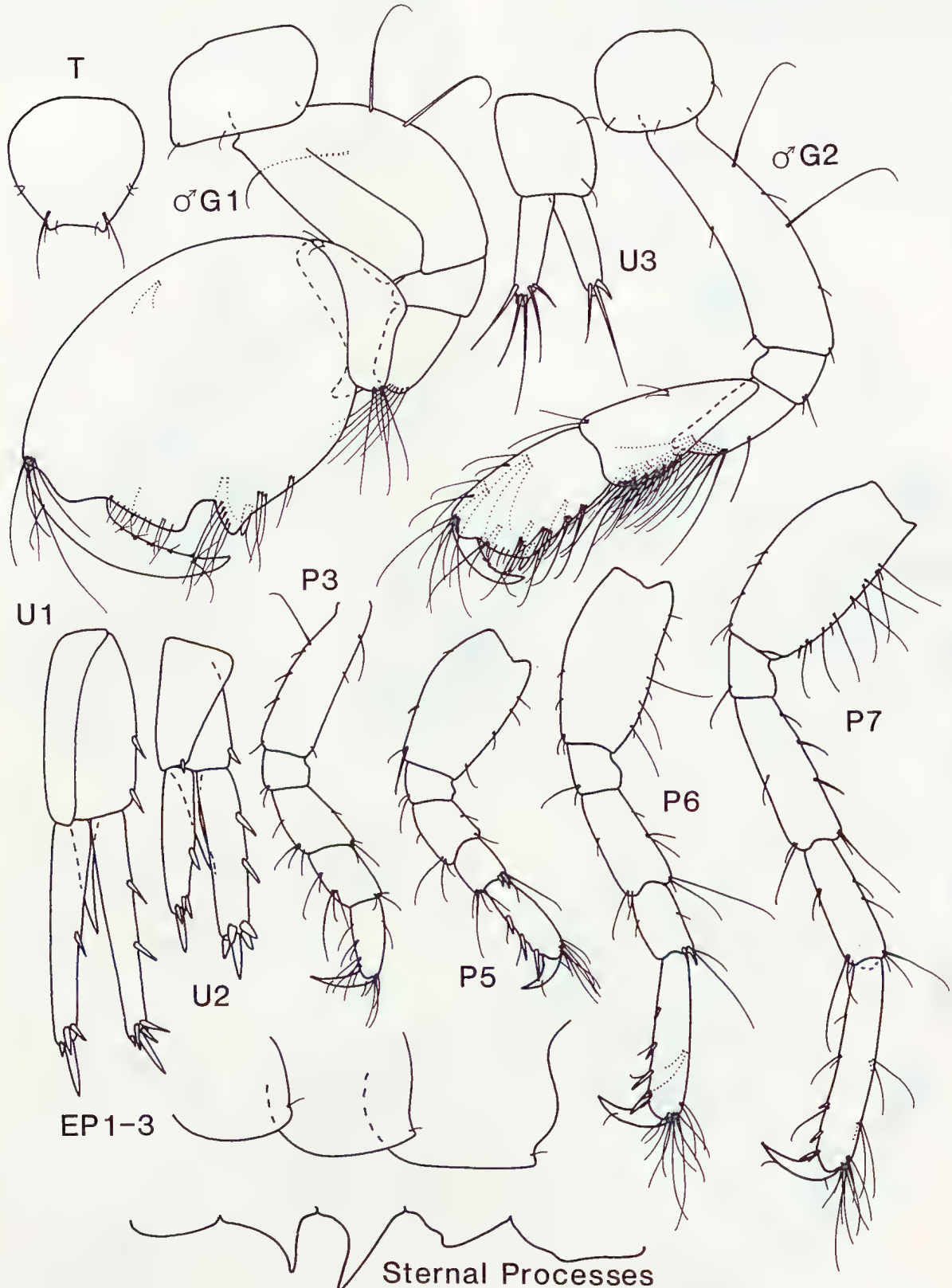


Fig.8. *Bemlos ephippium* n.sp., male, Lizard Island.

Description. Body (in alcohol) with saddles of dense brown pigment on the dorsum of the head, pereon segments 2-7 and pleon segments 1-3. Male pereon segments 2-3 with strong, acute, midventral sternal processes, pereon segment 4 with small rounded process. Head anteroventral margin only moderately produced, subacute. Labium outer plate

distal margin with 3 spines. Mandible palp article ratios 3 : 5 : 7, article 3 posterior margin weakly concave, setiferous over three quarters its length with marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 5 distal spines. Antenna 1 about three quarters body length, peduncular articles in the length ratios 7 : 9 : 3; accessory flagellum strongly

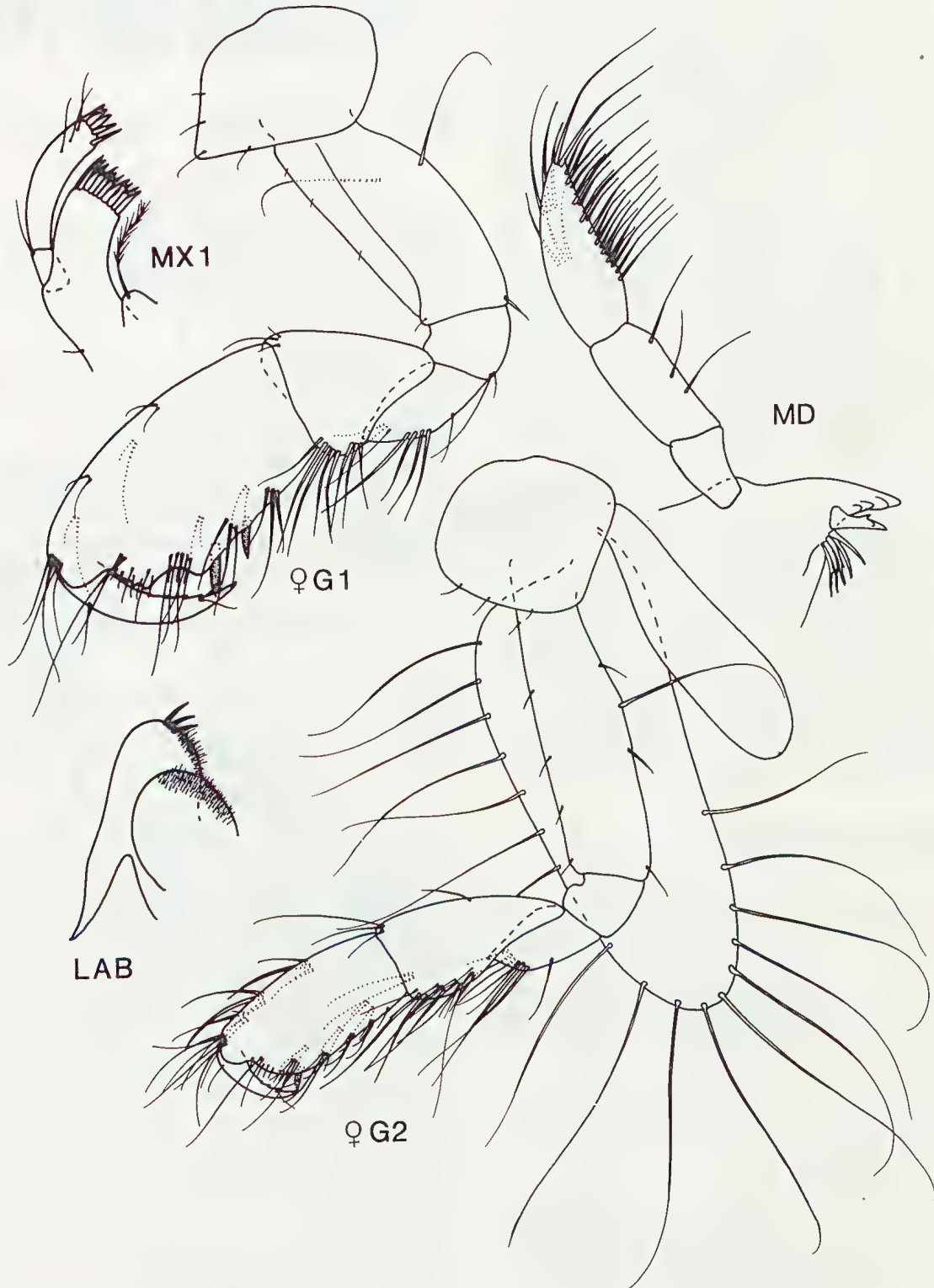


Fig.9. *Bemlos ephippium* n.sp., male female, Lizard Island.

developed with 7 articles; primary flagellum one and one half times length of peduncle with up to 16 articles. Antenna 2 two thirds length of antenna 1, peduncular article 5 longer than article 4; flagellum shorter than peduncular article 5 with about 4 articles. Male gnathopod 1 coxa subquadrangular, anterodistal corner a right-angle; basis robust, anterior margin weakly convex with a proximal nipple-like projection, posterior margin strongly convex; carpus greatly reduced, cup-shaped; propodus massive, about 5 times length of carpus and about three quarters as broad as long, palm with triangular excavation of moderate depth, defined by a broad, triangular tooth, proximal to which is a spine; dactylus stout, fitting palm. Female gnathopod 1 coxa somewhat produced anterodistally; basis stout; carpus of moderate size, triangular; propodus parallel-sided, twice length of carpus, palm sinuous with short crenulate anterior portion and evenly excavate posterior portion, posterior margin with 2 mediobasal spines, dactylus overlapping palm. Male gnathopod 2 basis slender, anterior margin concave, posterior margin convex; carpus elongate, slightly longer than propodus; dactylus fitting palm. Female gnathopod 2 basis only moderately slender, anterior margin straight, posterior margin only weakly convex; carpus and propodus subequal. Pereopods 3 and 4 sturdy, dactylus shorter than propodus. Pereopods 5–7 sturdy, in the length ratios 2 : 3 : 4; pereopod 7 less than two thirds length of body. Epimera 1–3 each with small posterodistal tooth. Uropod 1 peduncle with inter-ramal tooth less than half length of peduncle; rami subequal, longer than peduncle. Uropod 2 peduncle with inter-ramal tooth only slightly shorter than peduncle; inner ramus longer than outer and longer than peduncle. Uropod 3 rami short, subequal, scarcely longer than peduncle; outer ramus with small second article; margins of both rami lacking spines or setae, but with long distal setae.

Etymology. From the latin *ephippium* = saddle, referring to its pigmentation.

***Bemlos ehippium disjuncta* n.subsp.**

Fig. 10

Type material. HOLOTYPE: male, 4.0 mm. Red Bluff, Kalbarri, WA, 27°42'S 114°09'E, mixed algae and sediment, 3–4 m, 10 Jan 1984, R.T. Springthorpe, AM P37415. PARATYPES: 2 males, 2 females, type locality, AM P37416.

Additional material. Western Australia: 1 male, inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, brown alga, 1–5 m, 2 Jan 1984, R.T. Springthorpe, AM P37823.

Description. Differs principally from nominate form in the different pigmentation pattern: Pereon segments 1–7 and pleon segments 1–3 with paired dorsal blocks of dark brown pigment separated in the

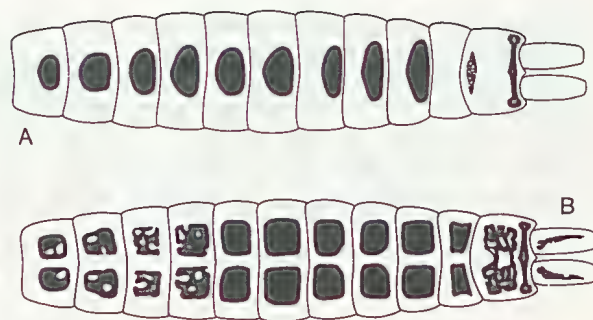


Fig.10. *Bemlos ehippium* n.sp., male, A. Lizard Island, B. Kalbarri.

midline. In hyperadult males the palmar excavation of gnathopod 1 is deeper and narrower than in the nominate form. Males of ssp. *disjuncta* were however larger (4.0 mm) than the males of the nominate form examined (2.8 mm).

Remarks. This species, in either form, is readily distinguished from all other known Australian *Bemlos* by the dense dorsal pigment bars.

Habitat. In algal turfs and reef rubble.

Distribution. Eastern Australia (Queensland and New South Wales) and Western Australia as two distinct subspecies. Not known outside Australia.

Etymology. From the latin *disiunctio* = separate, referring to the separate dorsal blocks of pigment.

***Bemlos australis* (Haswell)**

Figs 11–13

Microdeuteropus (sic) *australis* Haswell, 1879: 271, pl. 11, fig. 5.

Microdeutopus australis Haswell, 1882: 263.

Lembooides australis.—Stebbing, 1899: 350; 1906: 601.

Bemlos australis.—Myers, 1988: 188.

Material examined. Lizard Island, Queensland: 1 female, reefs at western end of lagoon, *Caulerpa racemosa* and *Halimeda micronesica*, 0–3 m, 5 Oct 1978, J.K. Lowry, C. Short, P.C. Terrill; 1 male, 12 females, lagoon entrance between Bird Islet and Trawler Beach, fine sand, 15 m, 5 Oct 1978, J.K. Lowry, P.C. Terrill; 1 male, 10 females, same locality, fine to coarse sand, 15 m, 5 Oct 1978, J.K. Lowry, P.C. Terrill; 1 female, fringing reef, between Bird Islet and South Island, *Halophila*, mixed algae, *Caulerpa*, *Halimeda* with coral rubble, predominated by platelet foraminifera, 24–27 m, 7 Oct 1978, J.K. Lowry; 1 male, 100 m off Freshwater Beach, sediment sample from sand bottom, 1.5 m, 10 October 1978, C. Short; 1 male, 3 females, inside lagoon entrance, between Bird Islet and Trawler Beach, drift and attached algae from sandy bottom, 10 m, 12 Oct 1978, P.C. Terrill; 1 male, off North Point, red algae and coral rubble from subtidal caves, 3–6 m, 14 Oct 1978, J.K. Lowry; 2 females, off North Point, mixed algal sample, 3–6 m, 14 Oct 1978, J.K. Lowry; 4 males, 9 females, reef edge, 200 m, north-west of Palfrey Island, sand sample off reef base, 12 m, 16 Oct 1978, J.K. Lowry; 5 males, 6 females, 119 mm, halfway between

Mangrove Beach and South Island, fine sediment, 10 m, 30 Sept 1978, A. Jones. New South Wales: 1 male, 2 females, Munganno Point, Twofold Bay, subtidal rock platform, 7 m, 10 Oct 1984, P. Hutchings, AM P36189; 3 females, Murrumbulga Point, Twofold Bay, subtidal rock platform, 5 m, 17 Sept 1985, S. Keable, P. Hutchings, AM P37479; 2 females, 1 male, Quarantine Bay, Twofold Bay, airlift from

Posidonia beds, 9 Oct 1984, S. Keable, J. van der Velde, AM P36031; 3 females, same locality, S. Keable, A. Reid, AM P37480; 2 males, same locality, sediment from *Posidonia* beds, 11 Dec 1984, S. Keable, E. Bamber, AM P37481; 9 males, 2 females, 3 mm, same locality, airlift from *Posidonia* beds, 28 Mar 1985, S. Keable, A. Paul, L. Walker, AM P37482; 13 females, 6 males, 5 mm, same

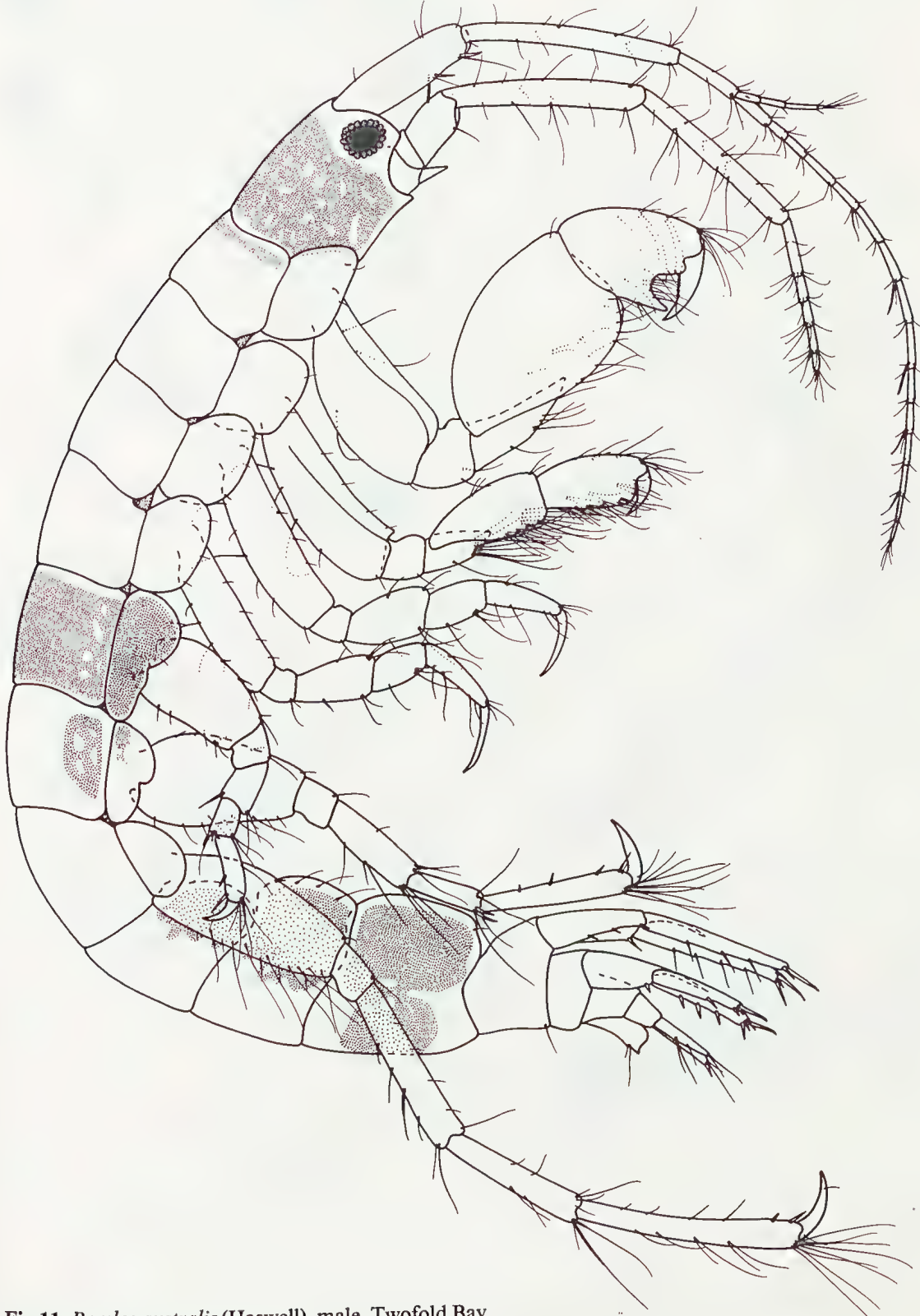


Fig.11. *Bemlos australis* (Haswell), male, Twofold Bay.

locality, 25 June 1985, S. Keable, A. Reid, AM P37483; 15 females, 11 males, same locality, 17 Sept 1985, S. Keable, P. Hutchings, AM P37484.

Description. Head, pereon segments 1 and 5-6+7 and pleon 1-3 with dense, irregular brown pigment (in alcohol), pigment extending on to coxae and

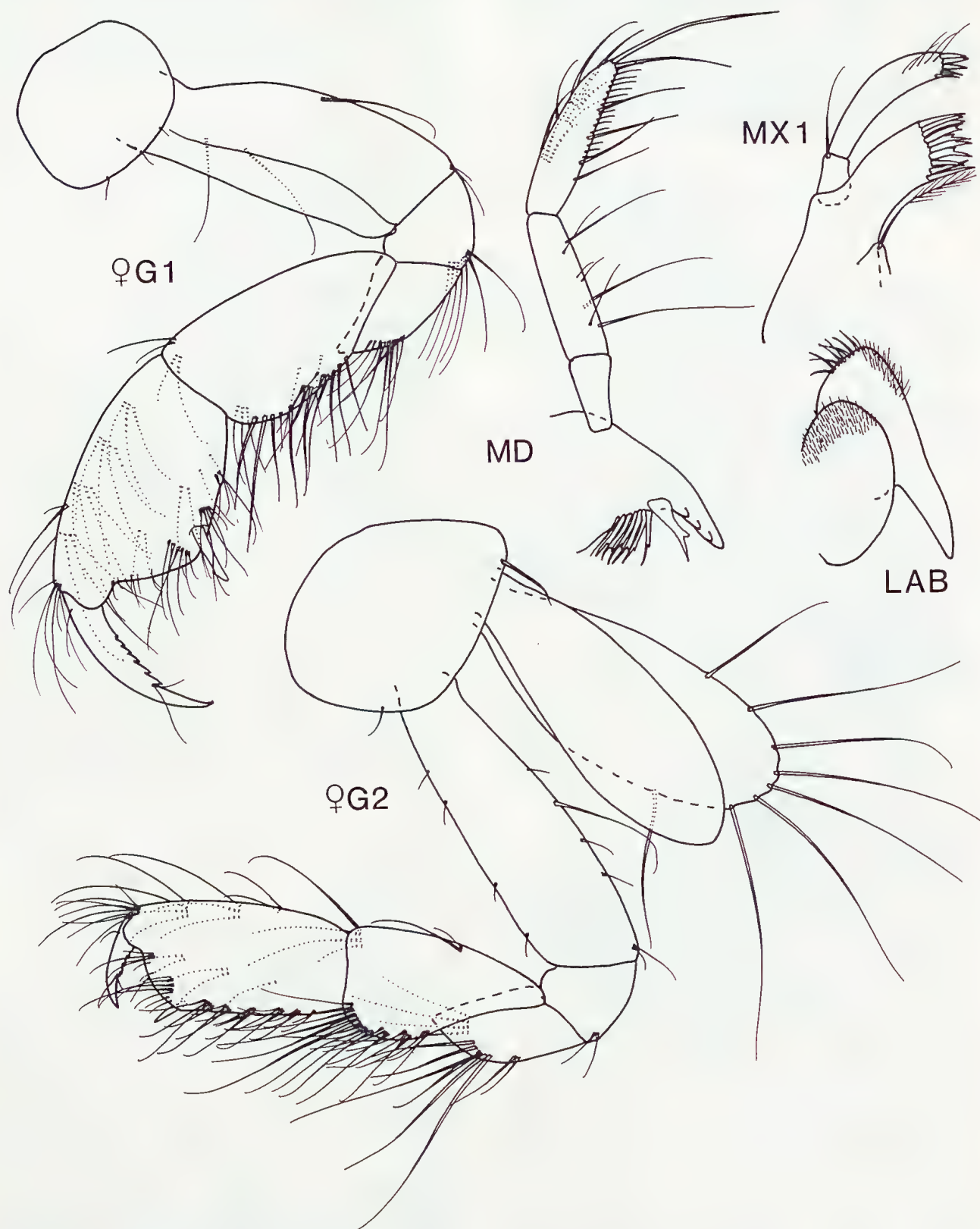


Fig.12. *Bemlos australis* (Haswell), male, female, Twofold Bay.

epimera. Male sternum without processes. Head anteroventral margin moderately produced, subacute. Labium outer plate, distal margin, with about 9 spines. Mandible palp article ratios 3 : 5 : 6; article 3 posterior margin almost straight, setiferous

over four fifths of its length with marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 5 spines. Antenna 1 two thirds body length; peduncular articles in the length ratios 2 : 3 : 1; accessory flagellum with 4 articles, the terminal

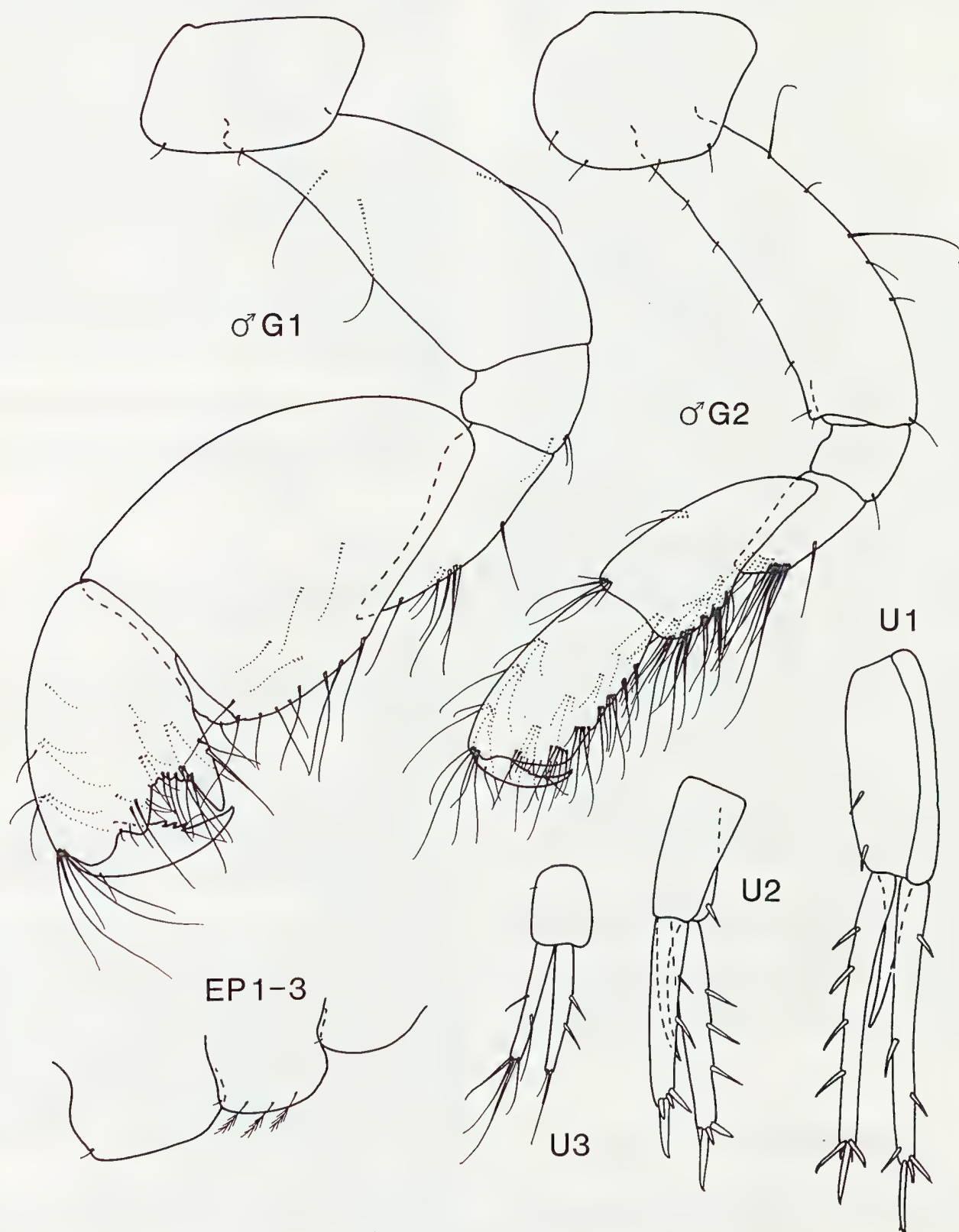


Fig.13. *Bemlos australis* (Haswell), male, Twofold Bay.

article rudimentary; primary flagellum longer than peduncle with up to 16 articles. Antenna 2 two thirds length of antenna 1; peduncular articles 4 and 5 subequal; flagellum a little shorter than peduncular article 5 with about 6 articles. Male gnathopod 1 coxa subquadrangular, anterodistal margin rounded; basis stout, anterior margin straight or weakly convex, posterior margin moderately convex; ischium elongate, over twice as long as broad; carpus enlarged, subovoid, one and one half times as long as broad; propodus two thirds length of carpus, broadening distally, palm deeply excavated, with short, almost transverse proximal palm remnant and strong posterodistal tooth; dactylus stout, slightly overlapping tooth. Female gnathopod 1 carpus and propodus subequal; palm evenly rounded; dactylus slender, overlapping palm. Male gnathopod 2 basis stout, anterior margin very weakly concave, posterior margin moderately convex; carpus and propodus subequal; dactylus slightly overlapping palm. Female gnathopod 2 similar to that of the male but carpus somewhat shorter than propodus. Pereopods 3 and 4 dactylus only a little shorter than propodus. Pereopods 5–7 in the length ratios 2 : 4 : 5; pereopod 7 scarcely half length of body. Epimera 1–3 rounded; epimeron 2 with ventral pectinate setae. Uropod 1 peduncle with inter-ramal tooth a little shorter than peduncle; rami subequal and longer than peduncle. Uropod 2 peduncle with inter-ramal tooth subequal with peduncle; inner ramus longer than outer and one and one half times length of peduncle. Uropod 3 rami subequal, elongate and slender; outer ramus with small second article; both rami with long terminal setae.

Remarks. This species superficially resembles species of *Lemboides* Stebbing in the enlarged, toothless carpus of the male gnathopod 1. This character is, however, due to convergence. *Bemlos australis* can be seen to differ from *Lemboides* species in the shape and setation of the mandibular palp, in the presence of multiple, rounded, molar plates as revealed by S.E.M. (see Myers, 1988) and by the presence of long distal setae on the rami of uropod 3. All these characters align the species with *Bemlos* Shoemaker.

Habitat. Appears to be rather eurytopic, occurring among *Posidonia*, algae, in coral rubble, fine sands and on a breakwater.

Distribution. Recorded from Queensland and New South Wales between Lizard Island in the north to Twofold Bay in the south. Not known outside Australia.

Bemlos aequimanus (Schellenberg)

Lembos aequimanus Schellenberg, 1938: 76, fig. 39;—Barnard, 1965: 527, fig. 26; 1970: 72, figs 36a–e;—

Ledoyer, 1984: 31, fig. 14;—Myers, 1985: 385, figs 246–248.

Bemlos aequimanus.—Myers, 1988: 188.

Material examined. Queensland: 2 males, Dingo beach, south-east of Bowen, 20°05'S 148°30'E, algal washings from muddy sand flats, 30 May 1977, I. Loch, AM P37821. New South Wales: 6 females, 2 males, Quarantine Bay, Twofold Bay, *Posidonia* infauna, 2 m, 11 Dec 1984, S. Keable, J. van der Velde, AM P36033; 1 male, same locality, airlift, *Posidonia* beds, 9 Oct 1984, S. Keable, J. van der Velde, AM P37474; 3 females, same locality, 25 June 1985, AM P37475; 3 males, 13 females, same locality, 17 Sept 1985, AM P37476; 1 female, Murrumbulga Point, Twofold Bay, subtidal rock platform, 2–9 m, 11 Dec 1984, S. Keable, AM P36180; 7 females, same locality, kelp holdfasts on subtidal breakwater wall, 29 Mar 1985, S. Keable, A. Paul, L. Walker, AM P37477; 1 female, same locality, 17 Sept 1985, AM P37478. Victoria: 1 male, 15 females, Crib Point, Western Port, 38°20.83'S 145°13.49'E, 13 m, sandy gravel, 23 Mar 1965; 8 males, 11 females, 251 m, Crib Point, 38°20.29'S 145°14.18'E, 10 m, sandy gravel, 10 Mar 1965. South Australia: 2 males, Stokes Bay, Kangaroo Island, 7 m, 4 March 1978, I. Loch, AM P37822.

Habitat. Among algae and phanerogammes in shallow water.

Distribution. Widely distributed in western Pacific from Australia to Hawaii.

Bemlos quadrimanus (Sivaprakasam)

Fig. 14

Lembos quadrimanus Sivaprakasam, 1970: 81, fig. 1.

Lembos waipio.—Ledoyer, 1972: 200, pls 21A, 22, 24. (not *L. waipio* Barnard, 1970: 85, figs 44–45).

Lembos quadrimanus mozambicus Myers, 1975a: 359, figs 33–39.

Bemlos quadrimanus.—Myers, 1988: 188.

Material examined. Western Australia: 4 males, 6 females, Ned's Camp, Cape Range National Park, inshore limestone reef, brown algae, 1.5 m, 2 Jan 1984, R.T. Springthorpe, AM P37451; 6 males, 4 females, same locality, *Caulerpa* plus sediment, 1.5 m, 2 Jan 1984, J.K. Lowry, AM P37452.

Remarks. Myers (1974) erected a new subspecies of this species from Tanzania and Kenya based on the presence of a tooth on the merus and carpus of the female gnathopod 1. Western Australian material is identical to East African material in this respect, as also is material described by Ledoyer (1982) from Madagascar. In view of the wide distribution of this subspecies across the Indian Ocean, its status must be questioned. Sivaprakasam's (1970) material is unique in lacking these teeth and the possibility exists that they were overlooked.

Habitat. Among algae, sponges and coral.

Distribution. East Africa, Madagascar, India, Western Australia.

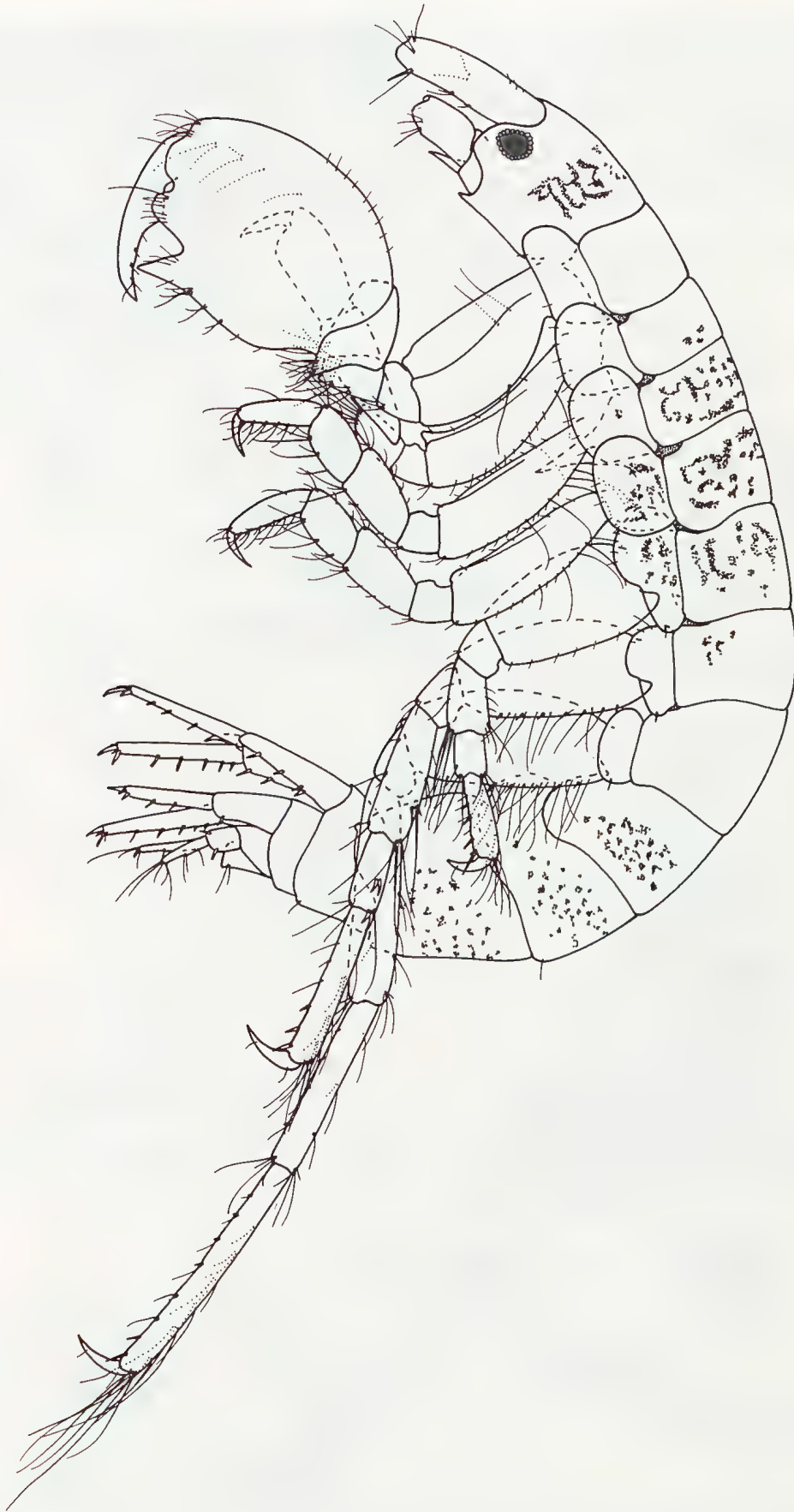


Fig.14. *Bemlos quadrimanus* (Sivaprakasam), male, Cape Range National Park.

***Bemlos saloteae* (Myers)**

Figs 15–16

Lembos saloteae Myers, 1985b: 373, figs 238–241; Myers
1986: 271, 288.

Bemlos saloteae Myers, 1988: 188.

Material examined. Queensland: 2 males, Lizard Island,
reef off North Point, coral rubble at base of cliff, 18 m, 13
Jan 1982, B. Kensley, AM P37417; 2 males, 4 females,



Fig.15. *Bemlos saloteae* (Myers), male, Lizard Island.

Lizard Island, between South Island and Palfrey Island, rubble with low algal turf from shallow ridge between islands, 1.5–2.5 m, 14 Jan 1982, B. Kensley, AM P37418; 1 male, 4 females, + 8 slides, Lizard Island, reef flat between Bird Island and South Island, algal encrusted rubble, 1.5–2.5 m, 16 Jan 1982, B. Kensley, AM P37419; 2 males, 1 female, Lizard Island, shelf between Palfrey Island and South Island, coarse sand and sediment, 0.5 m, 19 Jan 1982, B. Kensley, AM P37420; 1 male, 1 female, 3 km northwest of Nymph Island, 14°36'S 145°14'E, green algae, 15 m, 8 Feb 1979, AM P37421.

Remarks. Queensland material differs from Tongan material in the shape of the male gnathopod

1 propodus which in present material is less ovoid as a result of a straighter posterior margin. In addition, male gnathopod 2 is less elongate and the male sternal processes are less curved and restricted to segments 2–4 (2–5 in Tongan material). In all other characters including pigmentation, it agrees well with Tongan material and it does not seem sensible at this time to create a separate taxon for the present entity.

Habitat. Sand, reef rubble and algal turf.

Distribution. Tonga, Queensland.

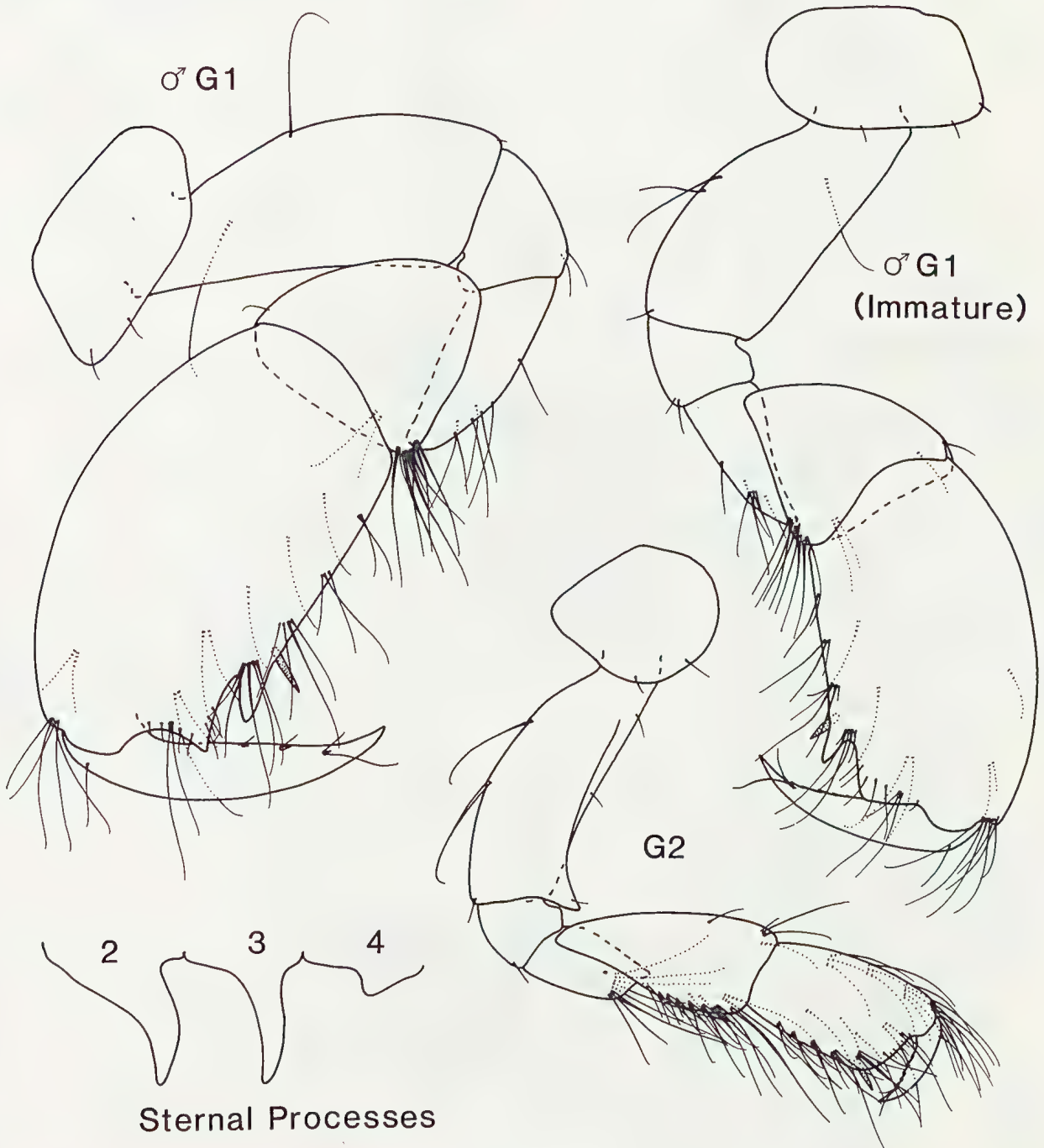


Fig.16. *Bemlos saloteae* (Myers), male, Lizard Island.

***Bemlos tridis* n.sp.**

Figs 17–19

Type material. HOLOTYPE: male, 5.0 mm, near Moona Moona Creek, Jervis Bay, NSW, with Ascidians, 3 m, 24 Apr 1982, P.B. Berents, AM P37422. PARATYPES: 1 male +

4 slides, AM P37423, 1 female, + 1 slide, AM P38609, 1 female, P38610, type locality.

Additional material. New South Wales: 2 females, 1 male, near Moona Moona Creek, Jervis Bay, with Ascidians, 4–6 m, 18 June 1982, P.B. Berents, AM P37424. South Australia: 1 male, Maston Point, American River,

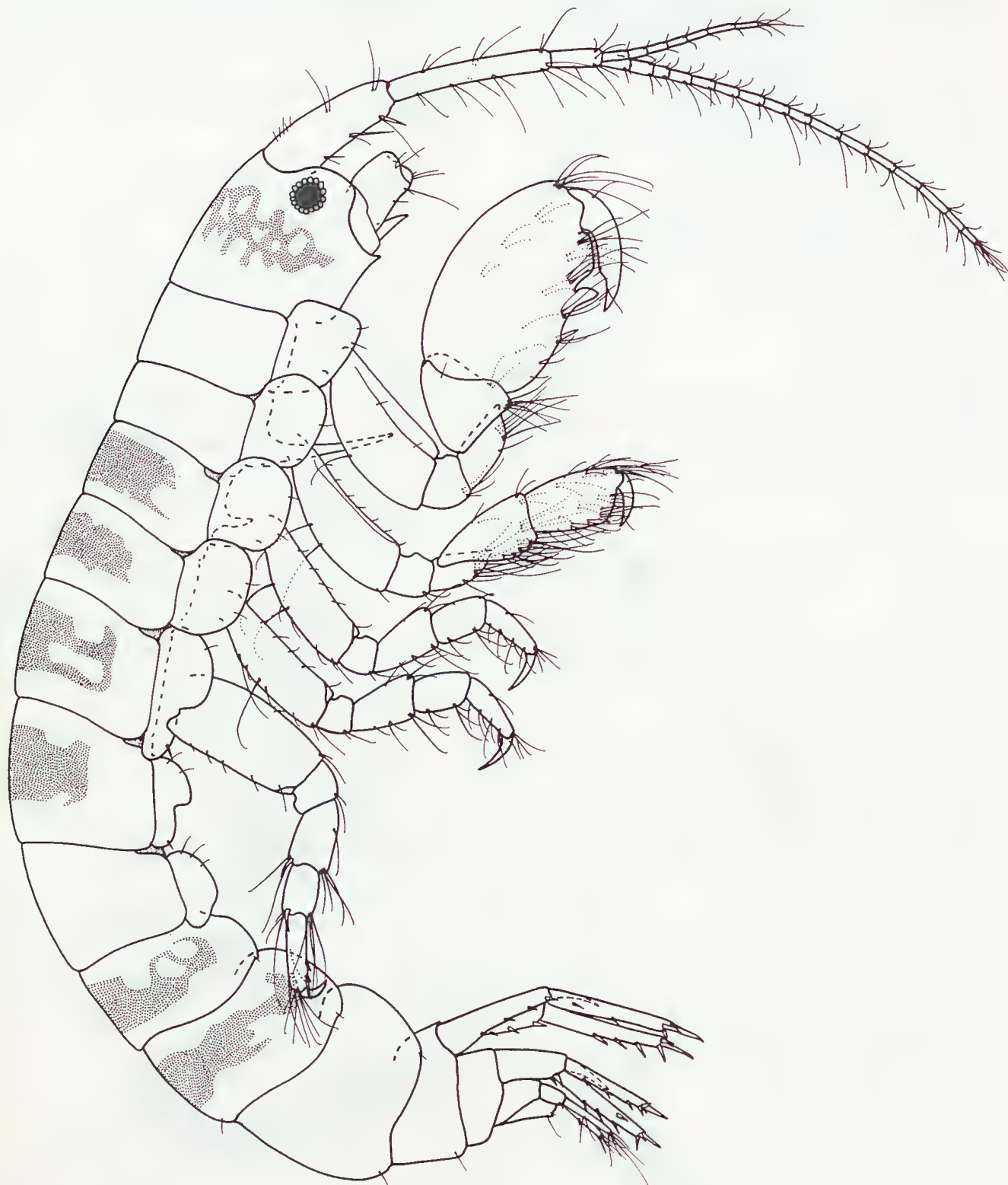


Fig.17. *Bemlos tridis* n.sp., male, Jervis Bay.

Kangaroo Island, clumps of sponge in channel below wharf, 4-5 m, 2 Mar 1979, P. Hutchings, AM P37425.

Description. Body (in alcohol) with broad bands of brown pigment on the dorsum of pereon segments 3-6 and pleon segments 2-3, the pigment bands

extending laterally onto the epimera, but not onto the coxae, head with reticulate pattern of brown pigment dorsally and laterally. Male pereon segment 2 with an extremely long, spear-like sternal process, segment 3 with a short acute process. Head anteroventral

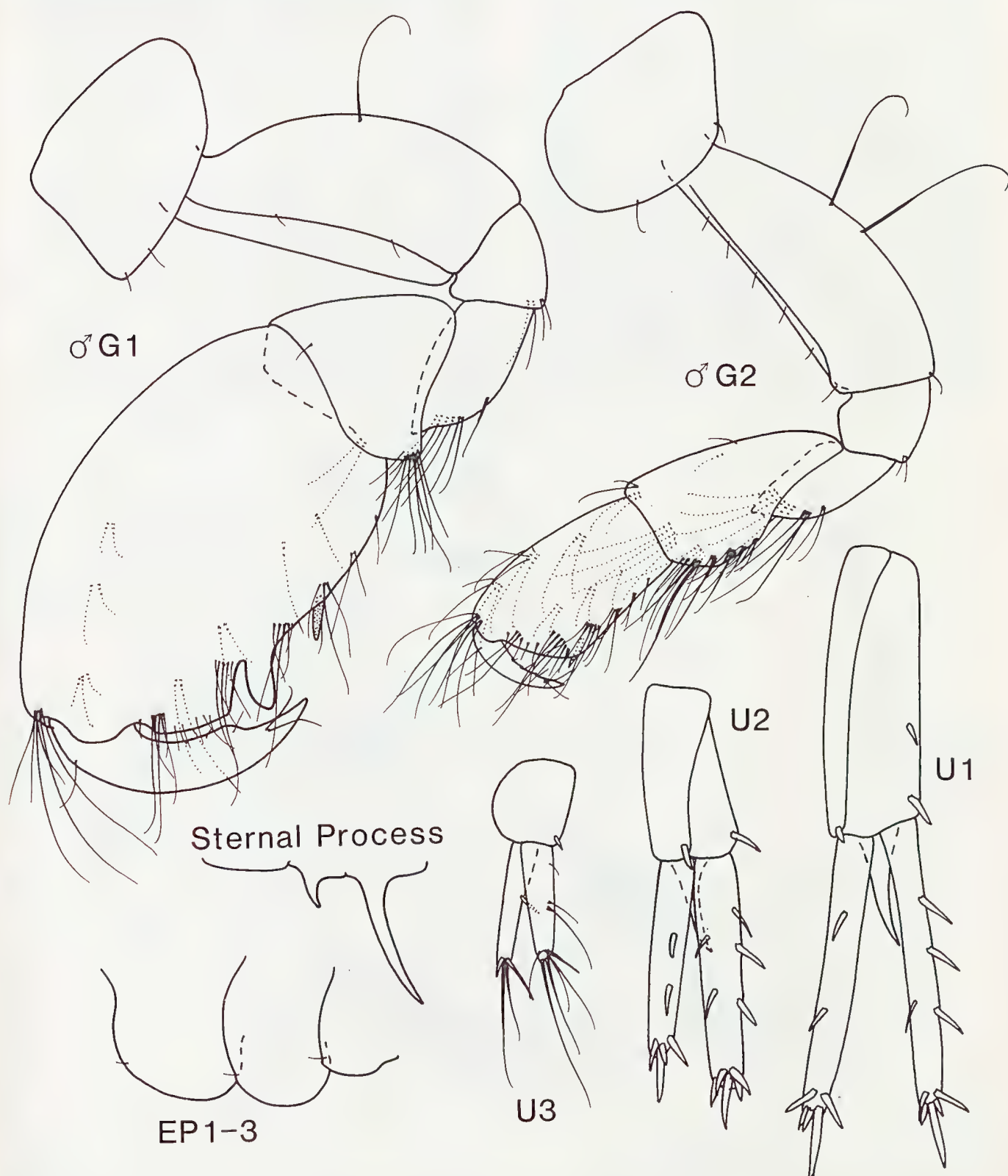


Fig.18. *Bemlos trudis* n.sp., male, Jervis Bay.

margin moderately produced, acute. Labium outer plate distal margin with about 10 spines. Mandible palp article ratios 3 : 5 : 8, article 3 posterior margin almost straight and setiferous over three quarters of its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 6 distal spines. Antenna 1 less than two thirds body length, peduncular articles in the length ratios 5 : 6 : 2; accessory flagellum with 8 articles, the terminal article rudimentary; primary flagellum a little longer than peduncle with about 17 articles. Antenna 2 missing in all specimens. Male gnathopod 1 coxa subquadrangular, anterodistal corner a rounded right-angle; basis stout; carpus triangular; propodus enlarged, almost 3 times length of carpus, subovoid, palm oblique, separated from a thumb-like posterodistal tooth by a deep narrow sinus, posterior margin with mediobasal spine; dactylus stout, posterior margin sinuous, overlapping palm. Female gnathopod 1 subsquare, carpus elongate; propodus a little longer than carpus, palm oblique; dactylus slender, overlapping palm. Male gnathopod 2 basis anterior margin straight, posterior margin convex; carpus slightly longer than propodus; dactylus slender, fitting oblique palm. Female gnathopod 2

carpus and propodus subequal. Pereopods 3 and 4 dactylus two thirds length of propodus. Pereopods 6–7 missing. Epimera 1–3 rounded. Uropod 1 peduncle with inter-ramal tooth less than half length of peduncle; rami slender, subequal and only a little shorter than peduncle. Uropod 2 peduncle with inter-ramal tooth over half length of peduncle; inner ramus stouter and longer than outer and one and one third times length of peduncle. Uropod 3 rami slender, subequal, one and one half times length of peduncle; outer ramus with small second article and long terminal setae.

Remarks. *Bemlos trudis* resembles *B. saloteae* but differs in the more oblique and obtuse ending palm, and short dactylus of the male gnathopod 1, in the absence of an anterodistal tooth on the basis of the male gnathopod 2, and not least in the extremely long and slender sternal process of pereon segment 2.

Habitat. Among ascidians and sponges in shallow water.

Distribution. New South Wales (Jervis Bay) and South Australia (Kangaroo Island).

Etymology. From the latin *trudis* = stake, referring to the long, stake-like pereon process of the male.

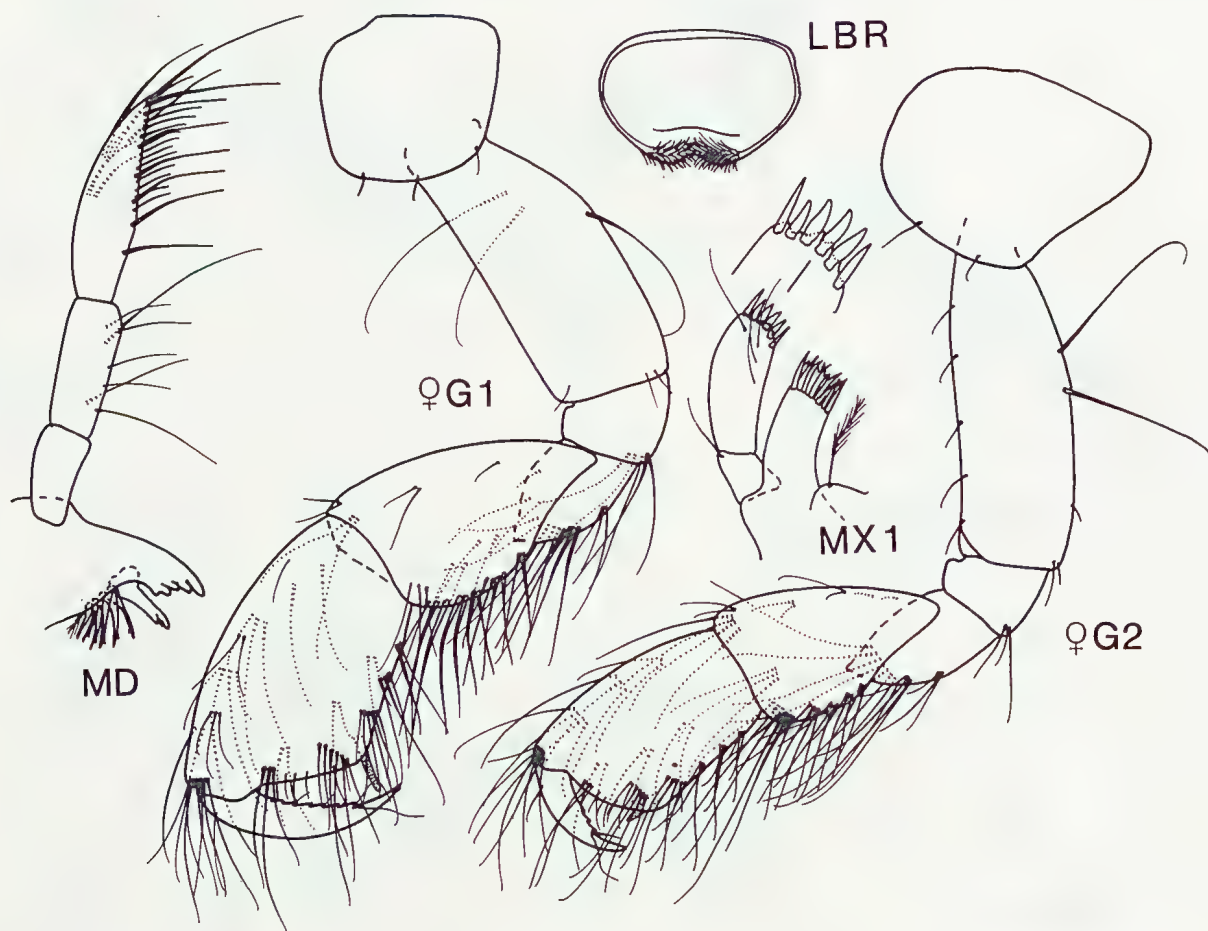


Fig.19. *Bemlos trudis* n.sp., male, female, Jervis Bay.

***Bemlos tridentatus* n.sp.**

Figs 20-21

Type material. HOLOTYPE: male, 2.8 mm, + 3 slides, Lizard Island, Qld, reef off North Point, coral rubble at base of cliff, 18.5 m, 13 Jan 1982, B. Kensley, AM P37426. PARATYPES: 2 females, AM P37427, 1 female + 3 slides, AM P38609, type locality.

Description. Body (in alcohol) without distinctive markings. Male pereon segments 3-5 with stout, forward facing sternal processes, that of segment 4 the longest. Head anteroventral margin unproduced, obtuse. Labium outer plate distal margin with about 7 spines. Mandible palp article ratios 7 : 8 : 10, article



Fig.20. *Bemlos tridentatus* n.sp., male, Lizard Island.

3 subovoid, posterior margin setiferous on distal half, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 5 distal spines. Antenna 1 slender, about two thirds body length; peduncular articles in

the length ratios 9 : 11 : 4; accessory flagellum with 3 articles, the third article rudimentary; primary flagellum subequal with peduncle, with about 9 articles. Male antenna 2 stout, peduncular article 3

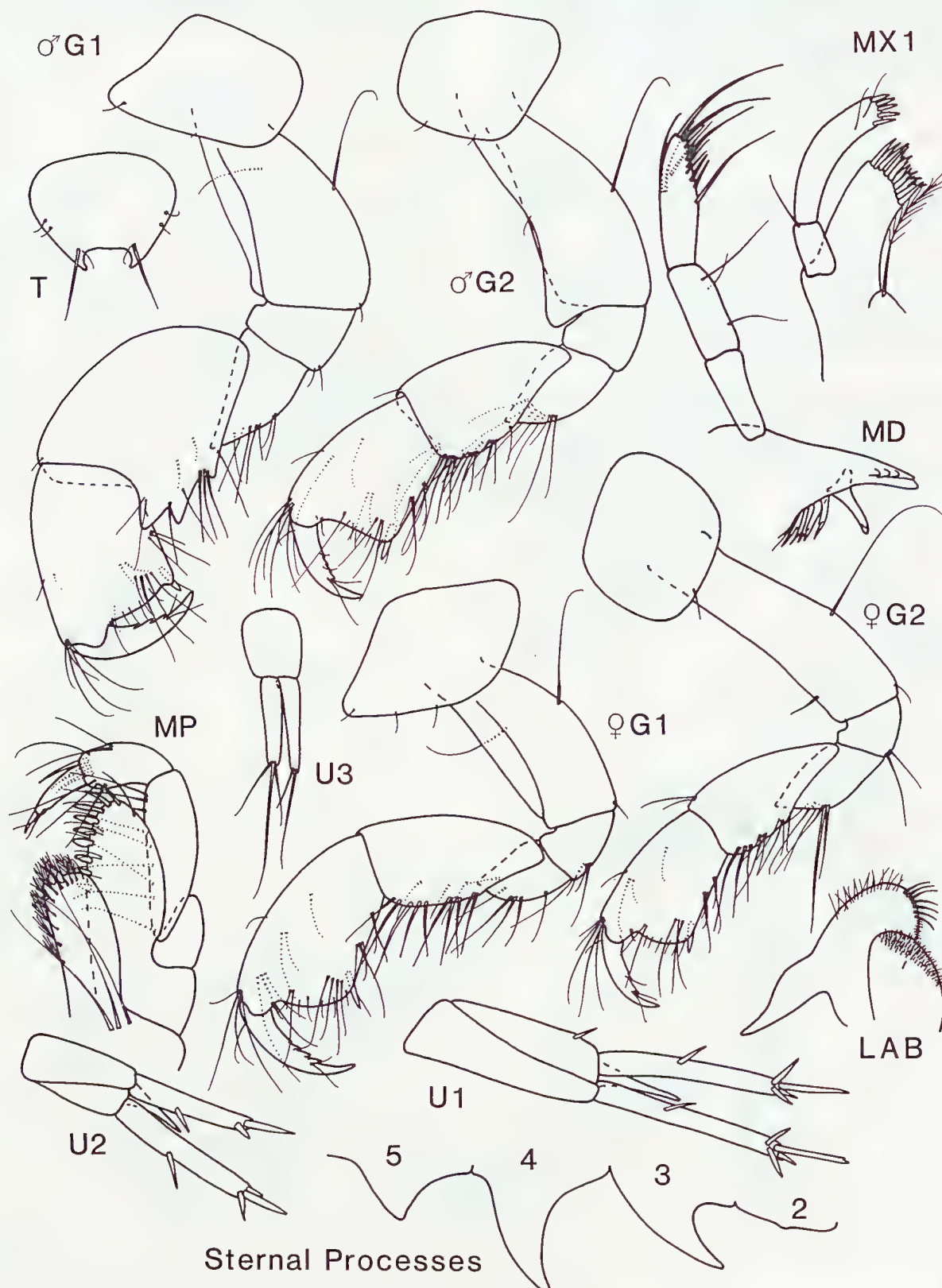


Fig.21. *Bemlos tridentatus* n.sp., male, female, Lizard Island.

swollen; article 4 broad; article 5 slender, but equal in length with article 4; flagellum shorter than peduncular article 5 with 3 articles. Female antenna 2 peduncular articles 3 and 4 not expanded, otherwise similar to that of male. Male gnathopod 1 coxa with anterodistal margin produced, rounded; basis stout, only a little longer than carpus; merus subtriangular; carpus enlarged, almost as broad as long, posterior margin with 3 triangular teeth, the most distal the longest, anterior margin strongly convex; propodus only a little shorter than carpus, widening distally, palm oblique, delimited by a small rounded process and a spine; dactylus scarcely overlapping palm. Female gnathopod 1 basis quite stout, but carpus and propodus slender, propodus a little longer than carpus, palm oblique, evenly rounded, delimited only by a spine; dactylus overlapping palm. Male gnathopod 2 basis expanded distally; carpus longer than propodus; propodus expanded distally, palm almost straight, forming a right-angle with posterior margin and delimited by a spine. Female gnathopod 2 basis elongate and slender; carpus and propodus subequal, palm evenly convex. Pereopods 3 and 4 dactylus only a little shorter than propodus. Pereopods 5–7 in the length ratios 2 : 3 : 5; pereopod 7 about two thirds body length. Epimera 1–3 rounded. Uropod 1 peduncle with inter-ramal process less than half length of peduncle; outer ramus a little longer than inner ramus and longer than peduncle. Uropod 2 peduncle with inter-ramal process over half length of peduncle; outer ramus shorter than inner ramus but a little longer than peduncle. Uropod 3 rami slender, longer than peduncle, lacking marginal spines and setae and with very long terminal setae which exceed length of rami.

Remarks. This species sits rather uneasily in the genus *Bemlos* with its sexually dimorphic antenna 2 with much reduced flagellum, and anteriorly produced, angular coxa 1 in the male. In the former character it resembles *Aorella* Myers, but differs in head shape, much shallower coxae and angular male coxa 1. The carpochele male gnathopod 1 is reminiscent of *Australomicrodeutopus* Myers (1988), but in that genus all three pairs of uropods are markedly different. For the present, pending further subdivision of the genus, *B. tridentatus* is most appropriately placed in the genus *Bemlos*.

Habitat. In coral rubble.

Distribution. As yet known only from the type locality.

Etymology. From the latin *tridens* = three teeth, referring to the three teeth on the male gnathopod 1 carpus.

Bemlos triangulum n.sp.

Figs 22–23

Type material. HOLOTYPE: male, 4.0 mm, + 1 slide. Sandbank reef, north Qld, 13°45'S 144°16'E, rubble washings from south-west end of reef, 8–10 m, 6 Dec 1982, I. Loch, AM P37428. PARATYPE: 1 female, + 3 slides; AM P37429, 2 females, AM P38612, type locality.

Description. Body (in alcohol) without distinct markings. Male pereon segments 2–3 with strong, straight, spiniform sternal processes, segment 4 with small nipple-like process. Head anteroventral margin produced, acute. Labium outer plate distal margin with about 11 spines. Mandible palp article ratios 9 : 6 : 3; article 3 subovoid, posterior margin weakly convex, setiferous on distal two thirds, setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Antenna 1 and 2 missing in all specimens. Male gnathopod 1 coxa anterodistal corner produced, subacute; basis massively swollen, scarcely longer than carpus; merus subtriangular; carpus enlarged, subovoid with posterodistal margin truncate; propodus equal in length to carpus but narrower, palm defined by a strong triangular tooth; dactylus overlapping palm. Female gnathopod 1 basis quite short, but carpus and propodus slender; propodus a little longer than carpus, palm oblique; dactylus overlapping palm. Male gnathopod 2 basis unexpanded; carpus and propodus subequal, palm oblique. Female gnathopod 2 scarcely differing from that of male. Pereopods 3 and 4 dactylus a little over two thirds length of propodus. Pereopod 5 basis broad. Pereopods 6 and 7 missing in all material available. Epimera 1–3 with small distoventral tooth. Uropod 1 peduncle with inter-ramal process less than half length of peduncle; outer ramus a little longer than inner and longer than peduncle. Uropod 2 peduncle lacking an inter-ramal process; outer ramus shorter than inner and scarcely longer than peduncle. Uropod 3 rami slender, longer than peduncle; inner ramus with 1 spine on inner margin; outer ramus with 1 seta on each of inner and outer margins and with a small second article; both rami with long terminal setae.

Remarks. This species appears to be closely related to the previous one, although it is not known whether antenna 2 is sexually dimorphic.

Habitat. Coral rubble.

Distribution. Known only from the type locality.

Etymology. From the latin *triangulus* = triangular, referring to the shape of the tooth on the male gnathopod 1 propodus.

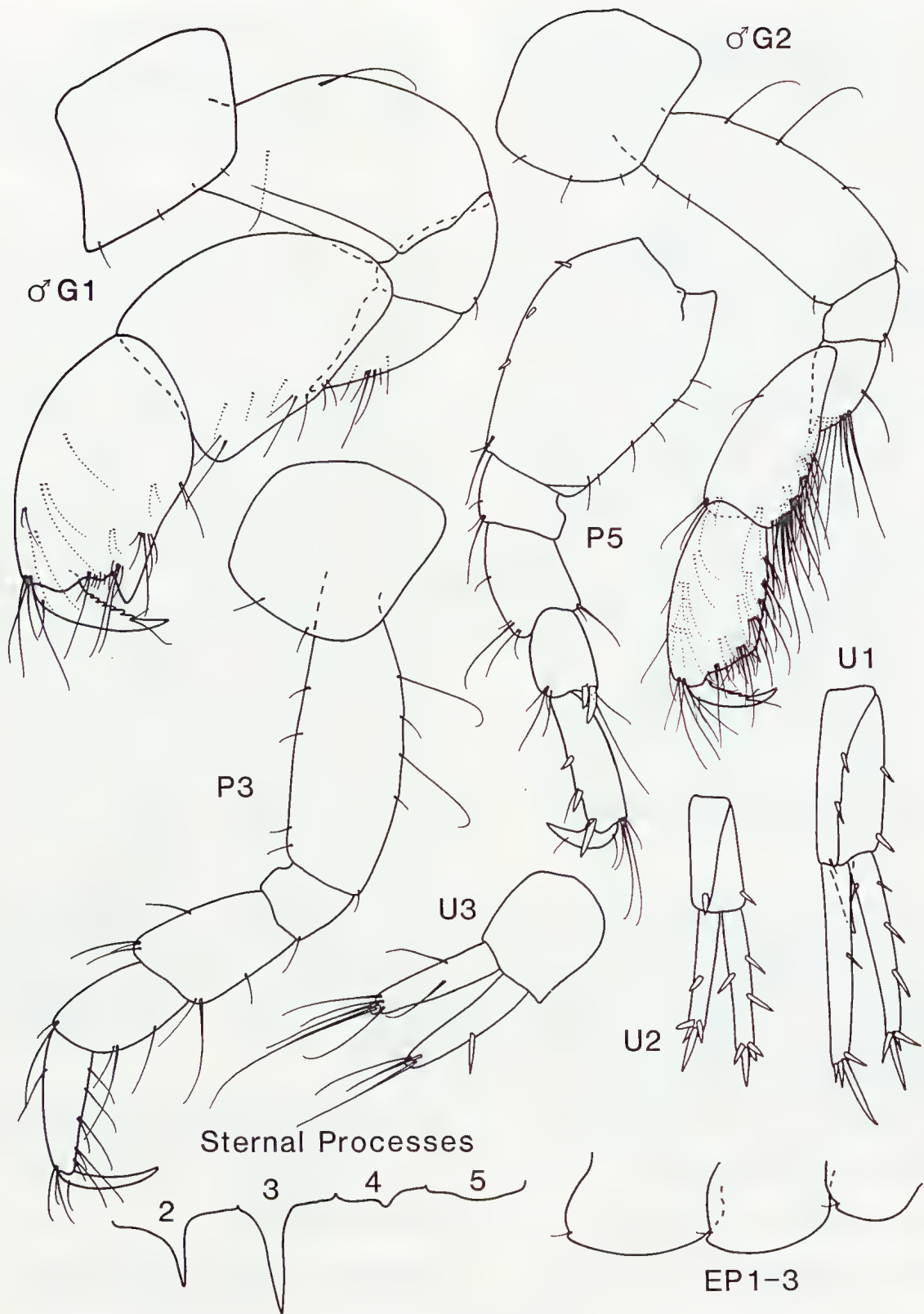


Fig.22. *Bemlos triangulum* n.sp., male, Sandbank reef.

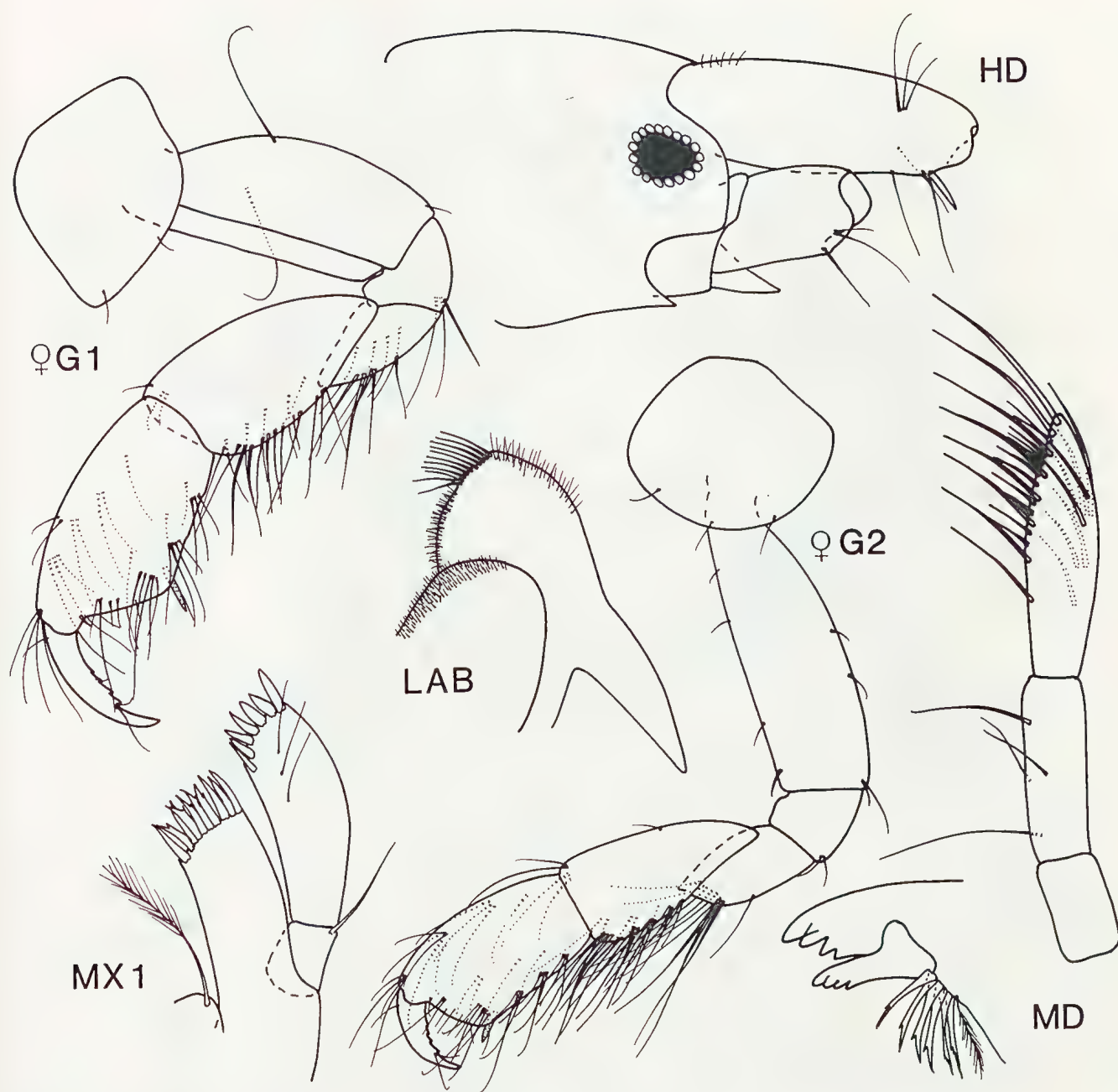


Fig.23. *Bemlos triangulum* n.sp., male, female, Sandbank reef.

***Bemlos bidens* n.sp.**

Figs 24–25

Type material. HOLOTYPE: male, 3.9 mm, + 4 slides. Great Detached Reef, near Raine Island, Qld, 11°43'S 144°03'E, reef flat, 10 m behind seaward face, 1–2 m, 10 Feb 1979, AMP37430.

Description. Body (in alcohol) with thin dorsal bands of brown pigment on pereon segments 2–4, and somewhat thicker dorsal bands on pereon segments 5 and 6 and pleon segment 2. The bands extend laterally but not onto coxae or epimera. Male pereon segments 2–4 with spiniform, acute, sternal

processes. Head anteroventral margin quite strongly produced, acute. Labium outer plate distal margin with 9 distal spines. Mandible palp article ratios 4 : 6 : 9; article 3 posterior margin straight and setiferous over two thirds of its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Antenna 1 and antenna 2 missing. Male gnathopod 1 coxa subquadrangular, evenly rounded anteriorly; basis stout; merus posterodistal margin produced into a long, acute tooth; carpus subtriangular, posterodistal margin produced into an acute tooth, shorter than that of merus; propodus over one and one half times length of carpus, palm



Fig.24. *Bemlos bidens* n.sp., male, Raine Island.

with shallow posterodistal depression resulting in defining obtuse tooth with a stout spine at its base; dactylus strongly overlapping palm. Male gnathopod 2 basis anterior margin weakly concave posterior margin moderately convex; carpus distinctly longer than propodus; dactylus slender, overlapping palm. Pereopods 3 and 4 missing. Pereopods 5-7 in the length ratios 4 : 6 : 9; pereopod 7 two thirds body length. Epimera 1-3 rounded. Uropod 1 peduncle with inter-ramal tooth a little over one thirds length of peduncle; rami slender; outer ramus a little longer than inner and subequal in length with peduncle. Uropod 2 peduncle with inter-ramal tooth a little less than two thirds length of peduncle; outer ramus slender, one and one third times length of peduncle;

inner ramus broken. Uropod 3 rami slender; outer ramus one and one half times length of peduncle with small second article and long terminal setae; inner ramus with marginal spines, broken distally. Female unknown.

Remarks. This species is clearly closely related to *B. virgus* from Fiji, but differs from that species in the presence of a carpal tooth on the male gnathopod 1, in lacking a brush of setae on the basis of that appendage and in lacking a truncate process on the inner face of the coxa of the male gnathopod 2.

Habitat. Unknown.

Distribution. Only known from type locality.

Etymology. From the latin *bidens* = two teeth, referring to the two teeth on the male gnathopod 1, one on the merus and one on the carpus.

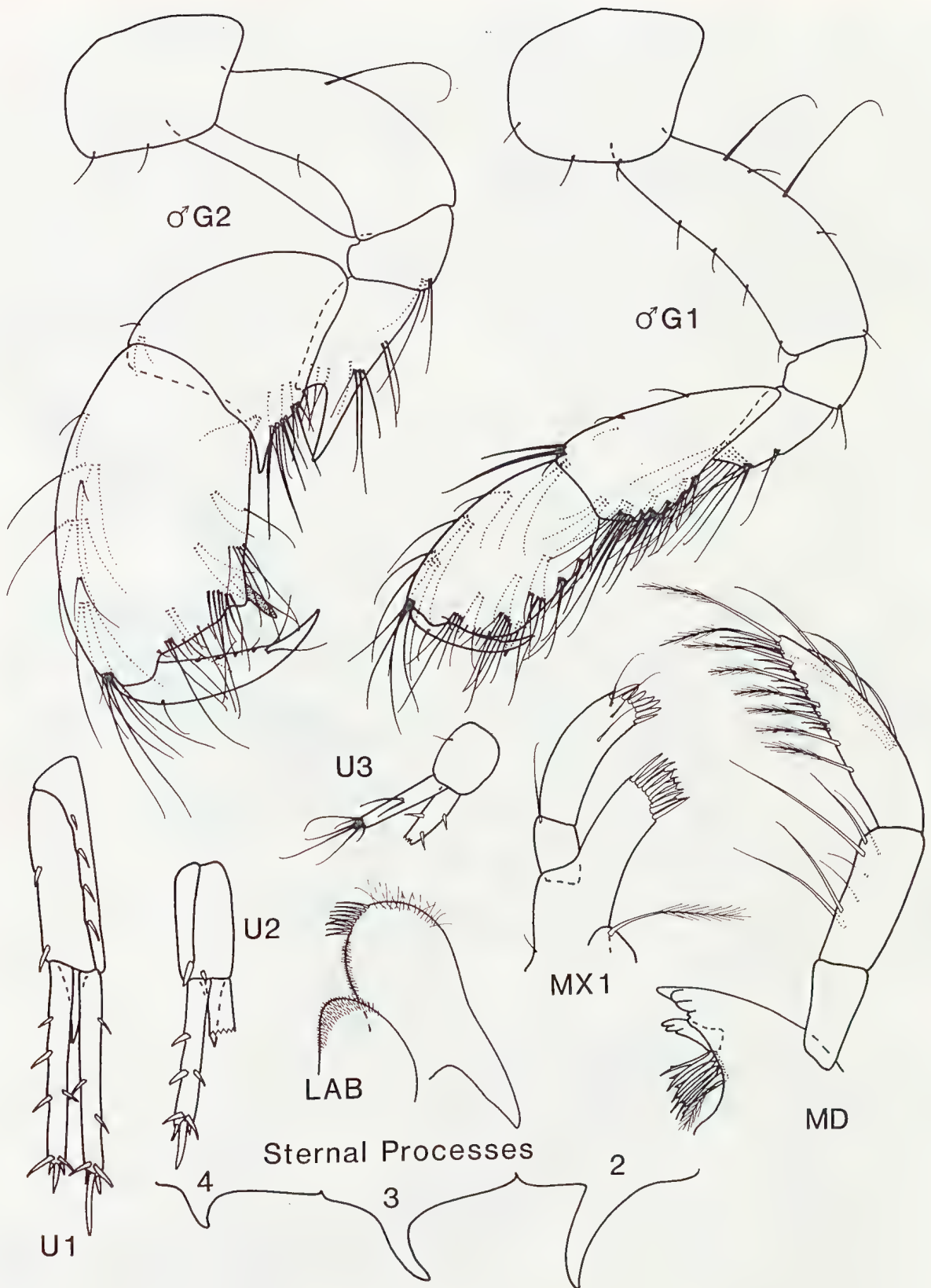


Fig.25. *Bemlos bidens* n.sp., male, Raine Island.

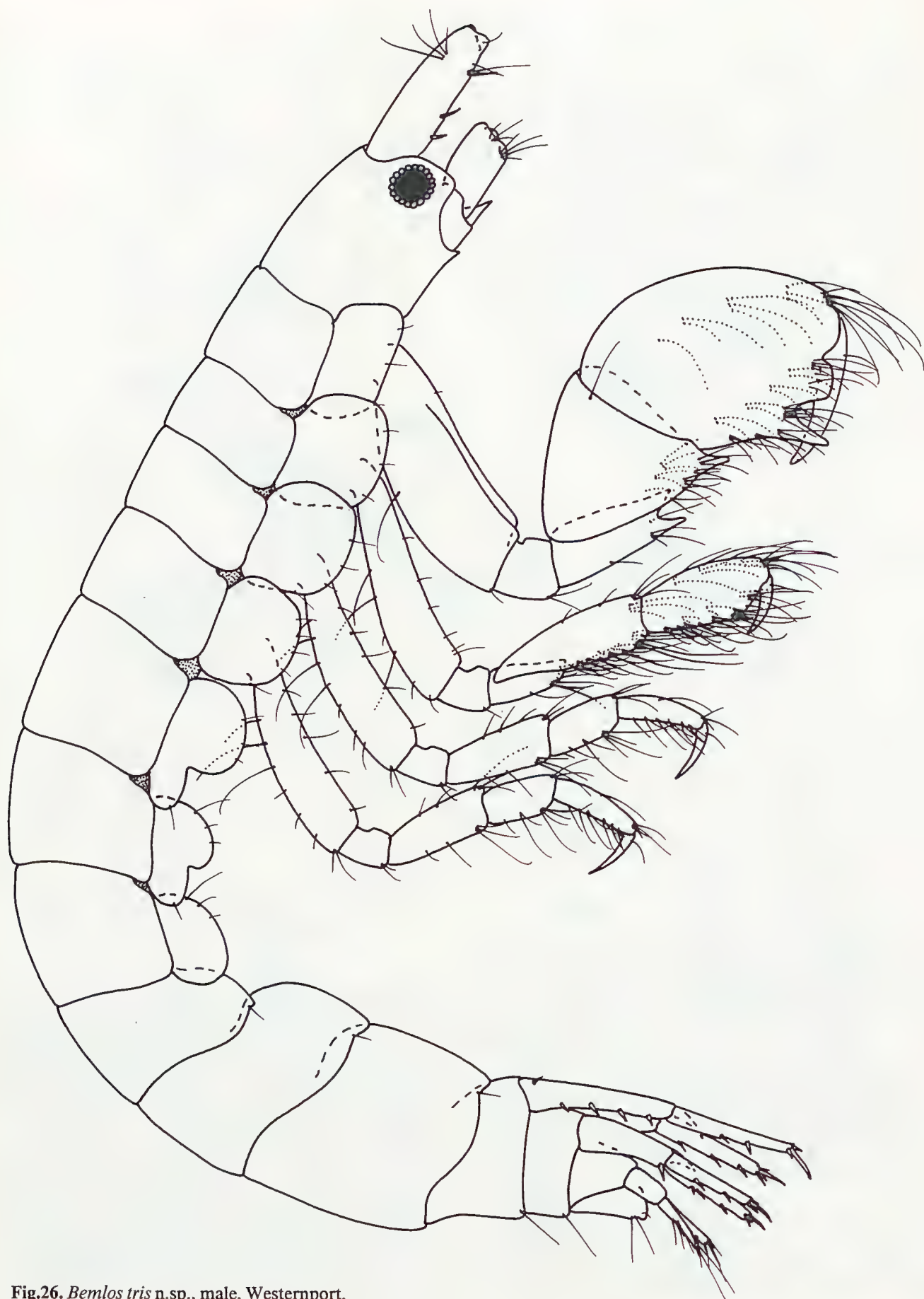


Fig.26. *Bemlos tris* n.sp., male, Westernport.

Bemlos tris n.sp.

Figs 26–28

Type material. HOLOTYPE: male, 4.4 mm. Westernport, Vic., 38°21.65'S 145°31.69'E, intertidal, 29 Jan 1974, NMV J14035. PARATYPES: 29 males, 82 females, + 4 slides, NMV J13611.

Additional material. Westernport, Victoria: 3 males, 11 females, 38°18.56'S 145°22.52'E, intertidal sand, 9 Jan 1974, NMV J13615; 6 males, 20 females, 38°15.31'S 145°22.38'E, intertidal sandy clay, 8 Jan 1974, NMV J13612; 1 female, 38°14.47'S 145°21.86'E, intertidal mud, 7 Jan 1974, NMV J13614; 1 male, 38°24.25'S 145°15.93'E, intertidal sand, 10 Jan 1974, NMV J13613; 1 male, 38°25.45'S 145°20.45'E, intertidal, silty-clay, 10 Jan

1974, NMV J13617; 5 males, 16 females, 38°22.90'S 145°31.83'E, intertidal sand-silt-clay, 24 Jan 1974, NMV J13606; 24 Jan 1974, NMV J13616; 2 males, 10 females, 38°29.19'S 145°21.34'E, 6 m, sand-silt-clay, 26 Nov 1973, NMV J13610; 1 male, 38°29.34'S 145°21.62'E, 6 m, sand-silt-clay, 26 Nov 1973, NMV J13609; 3 males, 3 females, 38°28.59'S 145°22.38'E, 6 m, sand, 26 Nov 1973, NMV J13607; 21 males, 40 females, 38°29.30'S 145°22.83'E, 6 m, 26 Nov 1973, NMV J13608; 7 males, 5 females, Crib Point, 38°22.29'S 145°13.41'E, 3 m, fine sand, 6 Apr 1965, NMV J13790; 2 males, 3 females, Crib Point, 38°21.73'S 145°13.23'E, 3 m, 1 Apr 1965, NMV J13792.

Description. Body (in alcohol) pale brown. Male pereon segments lacking sternal processes. Head anteroventral margin moderately produced

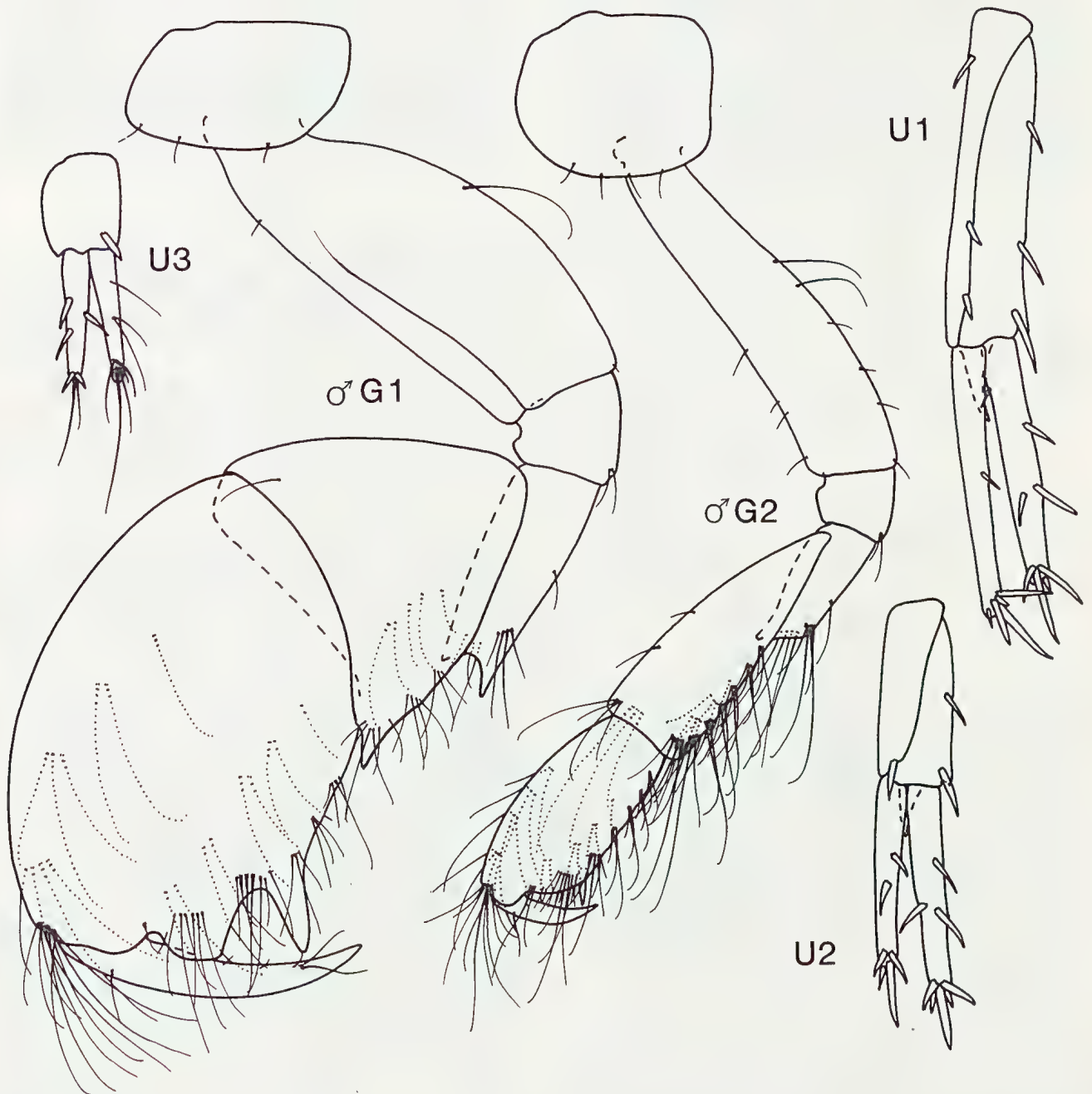


Fig.27. *Bemlos tris* n.sp., male, Westernport.

anteriorly, acute. Labium outer plate distal margin with 5 distal spines and a small compound coronate spine. Mandible palp article ratios 2 : 5 : 6, article 3 posterior margin falcate and setiferous over two thirds of its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Antenna 1 and 2 missing. Male gnathopod 1 coxa subquadrangular; basis moderately stout, anterior margin weakly sinuous, posterior margin moderately convex; merus elongate, posterodistal margin produced into a strong, acute tooth; carpus relatively large, triangular, posterodistal margin produced into an acute tooth; propodus one and one half times length of carpus, posterior proximal margin strongly convex, anterior proximal margin almost straight, palm stout, oblique, separated from dactylus hinge by a small sinus and from a strong, acute, posterodistal tooth, by a round-bottomed excavation; dactylus slender, elongate, overlapping posterodistal tooth. Female gnathopod 1 basis stout; carpus and propodus subequal, palm sinuous and defined by a weak tooth; dactylus slender, strongly

overlapping palm. Male gnathopod 2 elongate, slender; basis over 4 times as long as broad, anterior margin straight proximally, weakly concave distally, posterior margin weakly convex; carpus almost 3 times as long as its maximal width; propodus four fifths length of carpus, palm oblique, defined by a spine; dactylus moderately stout, overlapping palm. Female gnathopod 2 not markedly slender; carpus less than twice as long as broad; propodus a little longer than carpus, palm oblique, defined by a spine; dactylus scarcely overlapping palm. Pereopods 3 and 4 dactylus two thirds length of propodus. Pereopods 5–7 missing. Epimera 1–3 each with broad, rounded, distoventral tooth. Uropod 1 peduncle with interramal tooth less than one quarter length of peduncle; rami subequal, shorter than peduncle. Uropod 2 peduncle with inter-ramal tooth a little over one quarter length of peduncle; inner ramus longer than outer and longer than peduncle. Uropod 3 rami slender, subequal, about one and one half times length of peduncle; outer ramus with small second article.

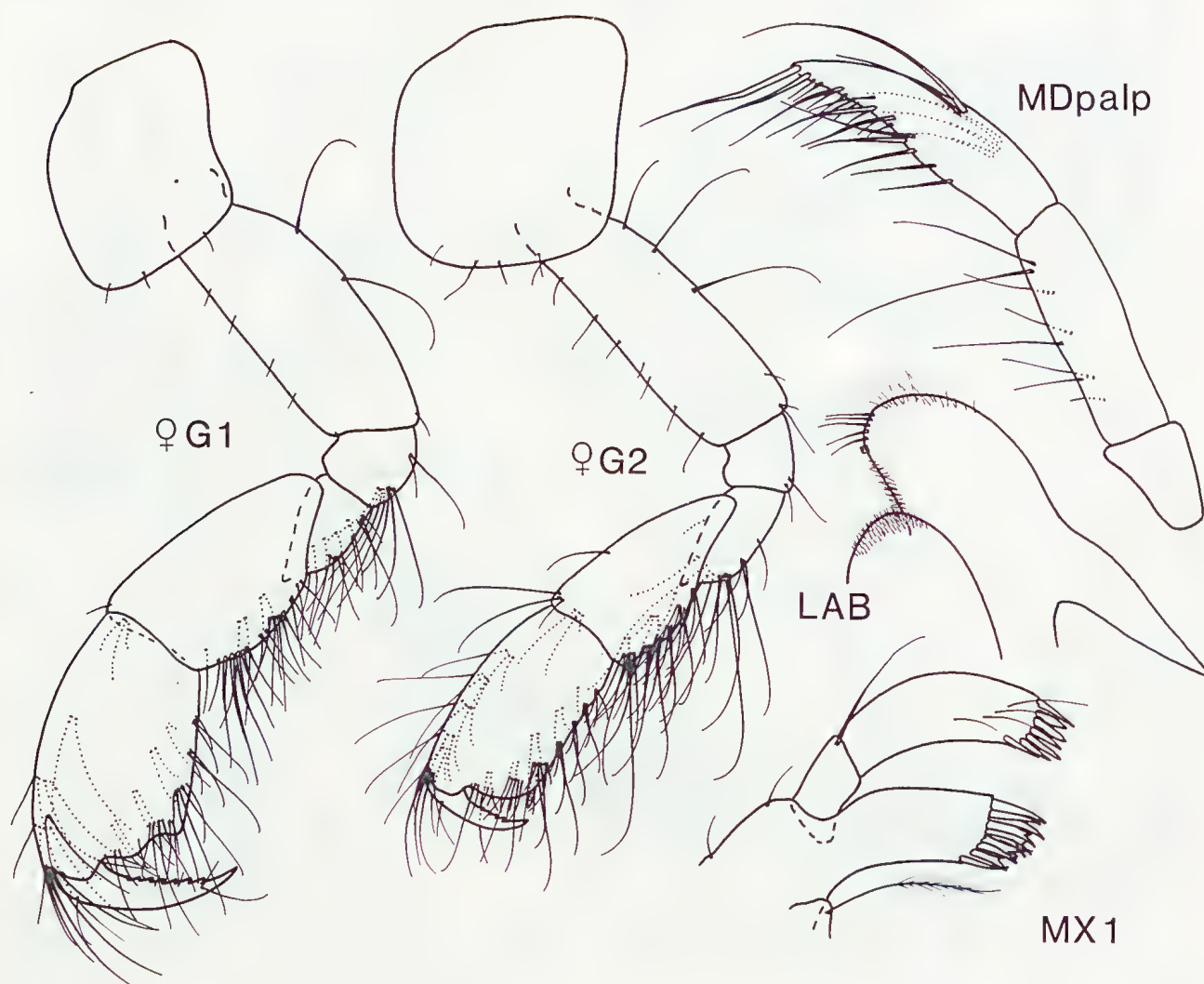


Fig.28. *Bemlos tris* n.sp., male, female, Westernport.

Remarks. This species resembles *B. bidens* but that species has a poorly excavate palm in the male gnathopod 1 and a relatively stout male gnathopod 2. It seems unlikely that the rather poorly known *B. bidens* is the subadult of *B. tris* as might be suspected from its smaller size and poorly developed propodus, since the meral tooth of *B. bidens* is very strongly developed by comparison with that of *B. tris*.

Bemlos tris also appears to be quite closely related to *B. tridens* (Schellenberg), from which it differs in the poorly setiferous male gnathopod 2 and to *B. quadrimanus* (Sivaprakasam) from which it differs in the much larger carpus of the male gnathopod 1, and from both species in lacking sternal processes.

Habitat. On muds and sands in the intertidal and to 6 m depth.

Distribution. Victoria.

Etymology. From the latin *tres* = three, referring to the three teeth on the male gnathopod 1, one on the merus, one on the carpus, one on the propodus.

***Bemlos dolichomanus* n.sp.**

Figs 29–31

Type material. HOLOTYPE: male, 4.3 mm. South-western Bass Strait (Victorian Institute of Marine Science Cruise 80-Sa-1, Stn 117, FV *Sarda*), 40°38.0'S 145°23'E, 36 m, muddy shell, 4 Nov 1980, G.C.B. Poore, NMV J14033. PARATYPES: 2 males, 2 females, + 6 slides, type locality, NMV J2459.

Additional material. 1 male, + 5 slides, Crib Point, Westernport, Vic., 38°20.29'S 145°14.18'E, sandy gravel, 10 Mar 1965m NMV J14039; 1 male, Bass Strait (Victorian Institute of Marine Sciences Cruise 81-T-1 NZ01, RV *Tangaroa* Stn 180), 39°12.9'S 146°27.3'E, 65 m, muddy sand, 18 Nov 1981, NMV J13701.

Description. Body (in alcohol) with brown bands of pigment on pereon segments 3, 4 and 7. Male pereon segment 2 with broad, triangular sternal process, pereon segments 3 and 4 each with nipple-like sternal process. Head anteroventral margin moderately produced, subacute. Labium outer plate distal margin with 7 simple spines and a compound coronate spine. Mandible palp article ratios 5 : 11 : 14, article 3 weakly falcate, setiferous over three quarters its length, with marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Antenna 1 missing. Antenna 2 slender, peduncular articles 4 and 5 subequal; flagellum subequal with peduncular article 5, with 8 articles. Male gnathopod 1 weakly setiferous, coxa subquadrangular; basis anterior margin weakly sinuous, posterior margin moderately convex; carpus stout, cup-shaped; propodus elongate, 3 times length of carpus, anterior margin weakly convex, posterior margin sinuous, palm short, straight almost transverse, separated from stout, triangular posterodistal tooth, by an asymmetrical, round-bottomed excavation, marginal spine some distance from posterodistal tooth; dactylus stout overlapping tooth and

opposable to spine. Female gnathopod 1 slender; carpus very slightly shorter than propodus; propodus with palm oblique, evenly convex and continuous with posterior margin, defined by a spine; dactylus in one female medially swollen, in the other female slender, in both cases, overlapping palm. Male gnathopod 2 basis anterior margin weakly concave, produced distally into triangular tooth, posterior margin moderately convex; carpus and propodus subequal, palm oblique; dactylus fitting palm. Female gnathopod 2 basis slender; propodus longer than carpus, parallel sided, palm oblique rather strongly convex; dactylus in one female swollen in the other relatively slender, fitting palm. Pereopods 3 and 4 propodus and dactylus very slender, dactylus over half length of propodus. Pereopods 5–7 missing. Epimera 1–3 each with small ventrodistal tooth, above which is inserted a small seta. Uropod 1 peduncle with inter-ramal tooth less than half length of peduncle; rami slender, subequal with each other and with peduncle. Uropod 2 peduncle with inter-ramal tooth about half length of peduncle; inner ramus longer than outer and longer than peduncle. Uropod 3 rami slender, the inner ramus the longer and distinctly longer than peduncle; outer ramus with small second article, at least 1 terminal seta longer than ramus.

Remarks. The shape of the male gnathopod 1 is quite distinctive. The peculiar expanded dactyls of gnathopods 1 and 2 in one of the two female specimens (as figured) may be an aberration rather than a species characteristic.

Habitat. On muddy sand and shell and sandy gravel in 10–65 m.

Distribution. Victoria.

Etymology. From the Greek *dolicho* = long; and *manus* = hand, referring to the long propodus of the male gnathopod 1.

***Bemlos strigilis* n.sp.**

Figs 32–34

Type material. HOLOTYPE: male, 4.3 mm. Cathedral Rock, Rottnest Island, WA, 32°01'S 115°27'E, red algae, 6 m, 21 Dec 1983, R.T. Springthorpe, AM P37431. PARATYPES: 3 males, 4 females, type locality, AM P37432. PARATYPES: 1 female + 3 slides, AM P38613, 1 male + 1 slide, AM P38614, 8 females, 2 males, AM P37433, 1 km west of Red Bluff, Kalbarri, 27°42'S 114°09'E, *Ecklonia* holdfasts, 18 m, 9 Jan 1984, J.K. Lowry; 1 male, 1 female, same locality and data, R.T. Springthorpe, AM P37434.

Additional material. South Australia: 1 male, Stokes Bay, north coast Kangaroo Island, algae on vertical rock face, 7 m, 4 Mar 1972, I. Loch, AM P37473.

Description. Body (in alcohol) with faint brown markings on dorsum of pereon segments 2–5 and 7 and pleon segments 1–2. Male pereon segments lacking sternal processes. Head anteroventral margin moderately produced, subacute. Labium outer plate distal margin with about 5 spines. Mandible palp



Fig.29. *Bemlos dolichomanus* n.sp., male, Bass Strait.

article ratios 3 : 6 : 9; article 3 posterior margin very weakly concave and setiferous over three quarters of its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 spines. Antenna 1 peduncular articles in the ratios 3 : 3 : 1; accessory flagellum broken, with 2+ articles; primary flagellum broken. Antenna 2 peduncular articles 4 and 5 subequal; flagellum subequal with peduncular article 5, with about 7 articles. Male gnathopod 1 coxa strongly produced forward, broadly rounded and down turned; basis enormous, anterodistal margin

expanded into rounded flange, bordered with stridulating ridges; inner face of basis with numerous long setae; carpus about as broad as long, anterior margin with stridulating ridges which rub against those of the basis anterior margin; propodus enormous expanded distally, palm with small sinus near dactylus hinge, with almost transverse anterior palmar portion followed by a deep triangular excavation in posterior portion and with defining triangular tooth lacking a spine in hyperadults; dactylus very robust scarcely overlapping palm.

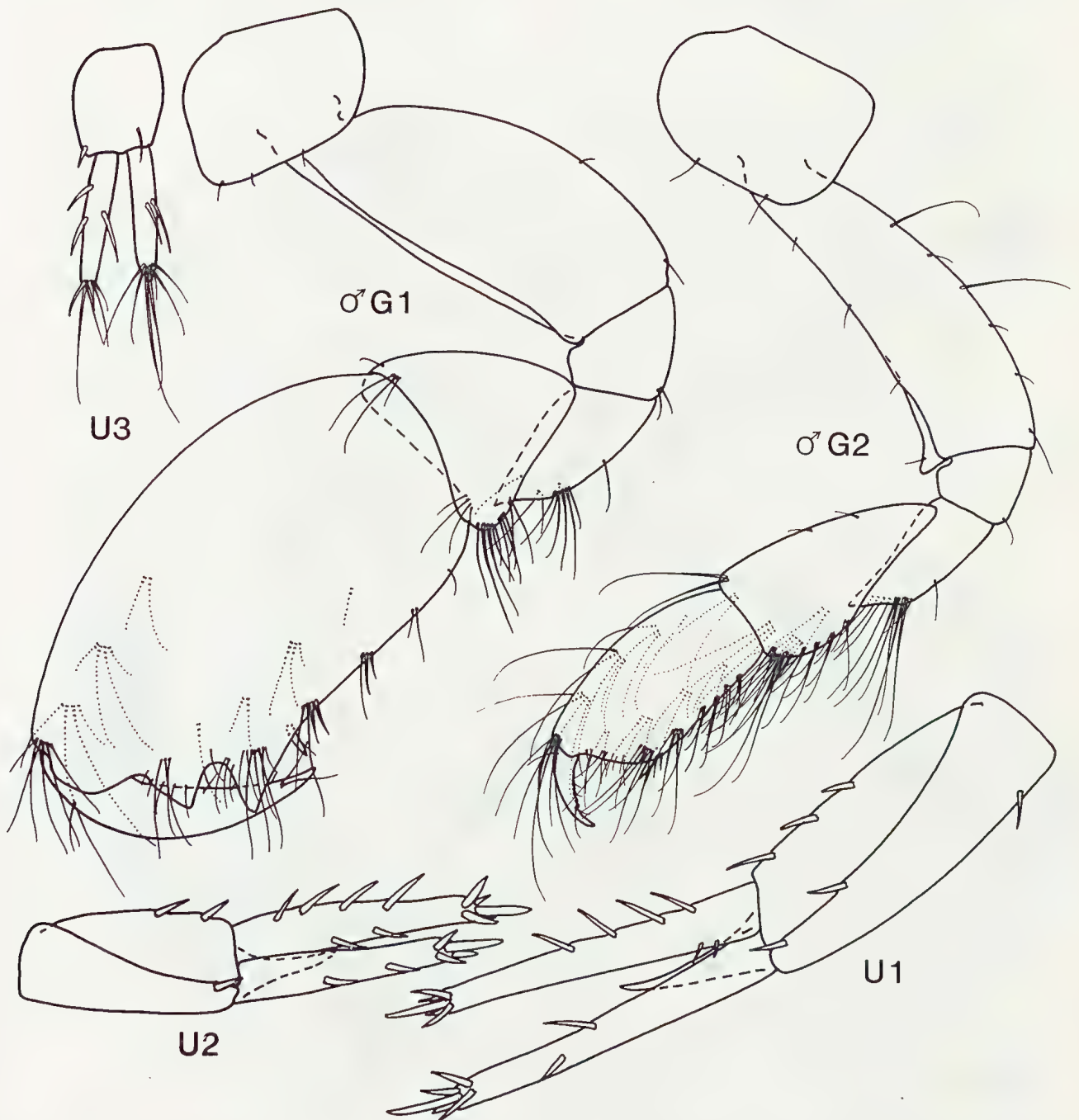


Fig.30. *Bemlos dolichomanus* n.sp., female, Bass Strait.

Female gnathopod 1 carpus longer than broad; propodus larger than carpus, parallel sided, palm sinuous; dactylus overlapping palm. Male gnathopod 2 basis about 3 times as long as broad; carpus and propodus elongate, slender; carpus slightly the longer; dactylus fitting palm. Female gnathopod 2 similar to that of male but less slender. Pereopods 3-4 sturdy, dactylus shorter than propodus. Pereopods 5-7 in the length ratios 2 : 4 : 6; pereopod

7 less than two thirds body length. Epimera 1-3 each with small posterodistal tooth. Uropod 1 peduncle with inter-ramal tooth about half length of peduncle; rami subequal, scarcely longer than peduncle. Uropod 2 peduncle with inter-ramal tooth about two thirds length of peduncle; inner ramus longer and straighter than outer. Uropod 3 rami short, subequal, scarcely longer than peduncle; outer ramus with small second article; rami with long terminal setae.

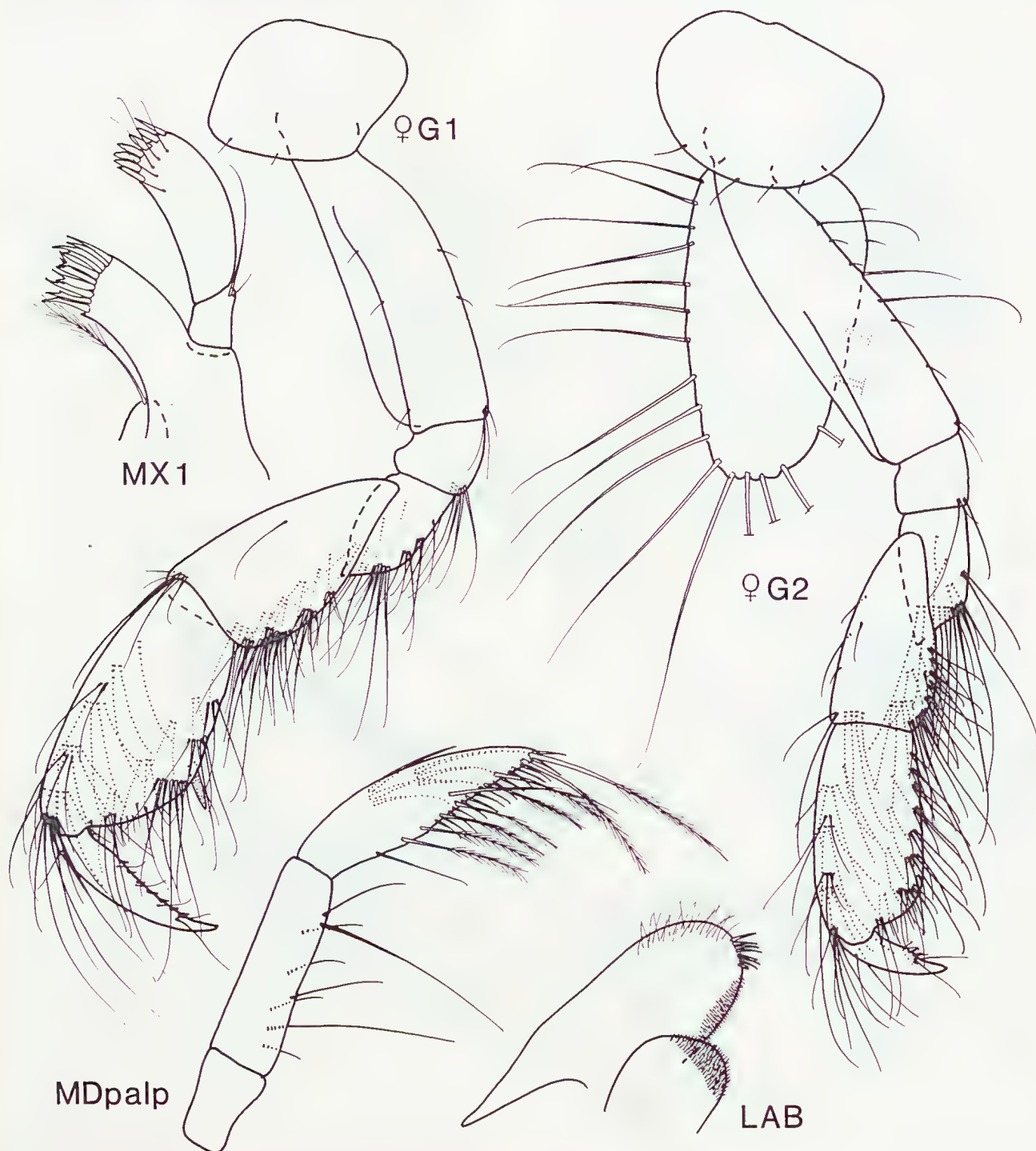


Fig.31. *Bemlos dolichomanus* n.sp., male, female, Bass Strait.

Remarks. This is the first species of *Bemlos* in which stridulating ridges have been described, nor is it known in any closely related genera, but is well known in *Grandidierella* spp., and in *Ericthonius* spp.

Habitat. Among algae in shallow water.

Distribution. Western Australia to South Australia.

Etymology. From the latin *strigilis* = scraper, referring to the stridulating ridges on the basis and carpus of the male gnathopod 1.



Fig.32. *Bemlos strigilis* n.sp., male, Rottneest Island.

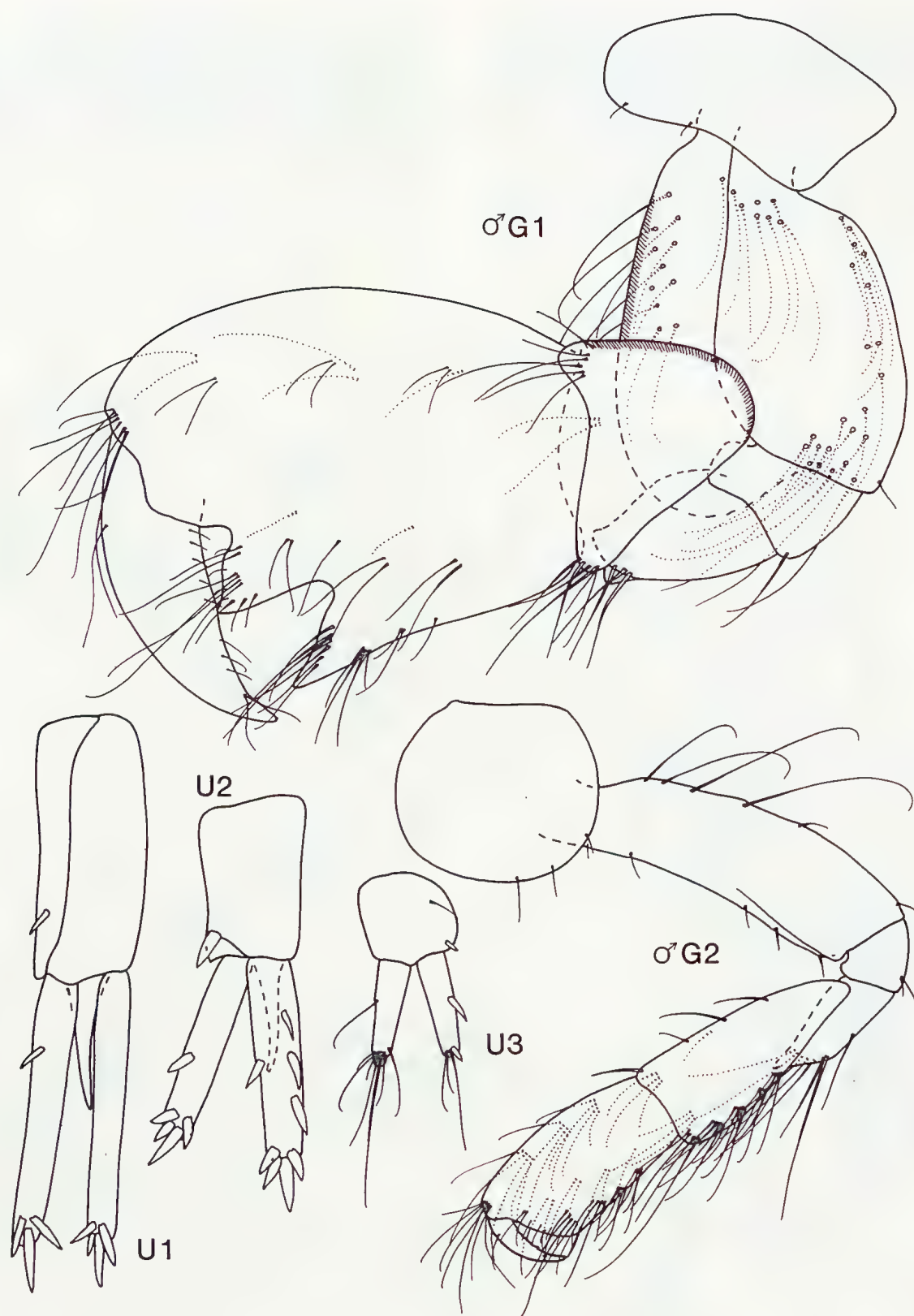


Fig.33. *Bemlos strigilis* n.sp., male, Rottnest Island.

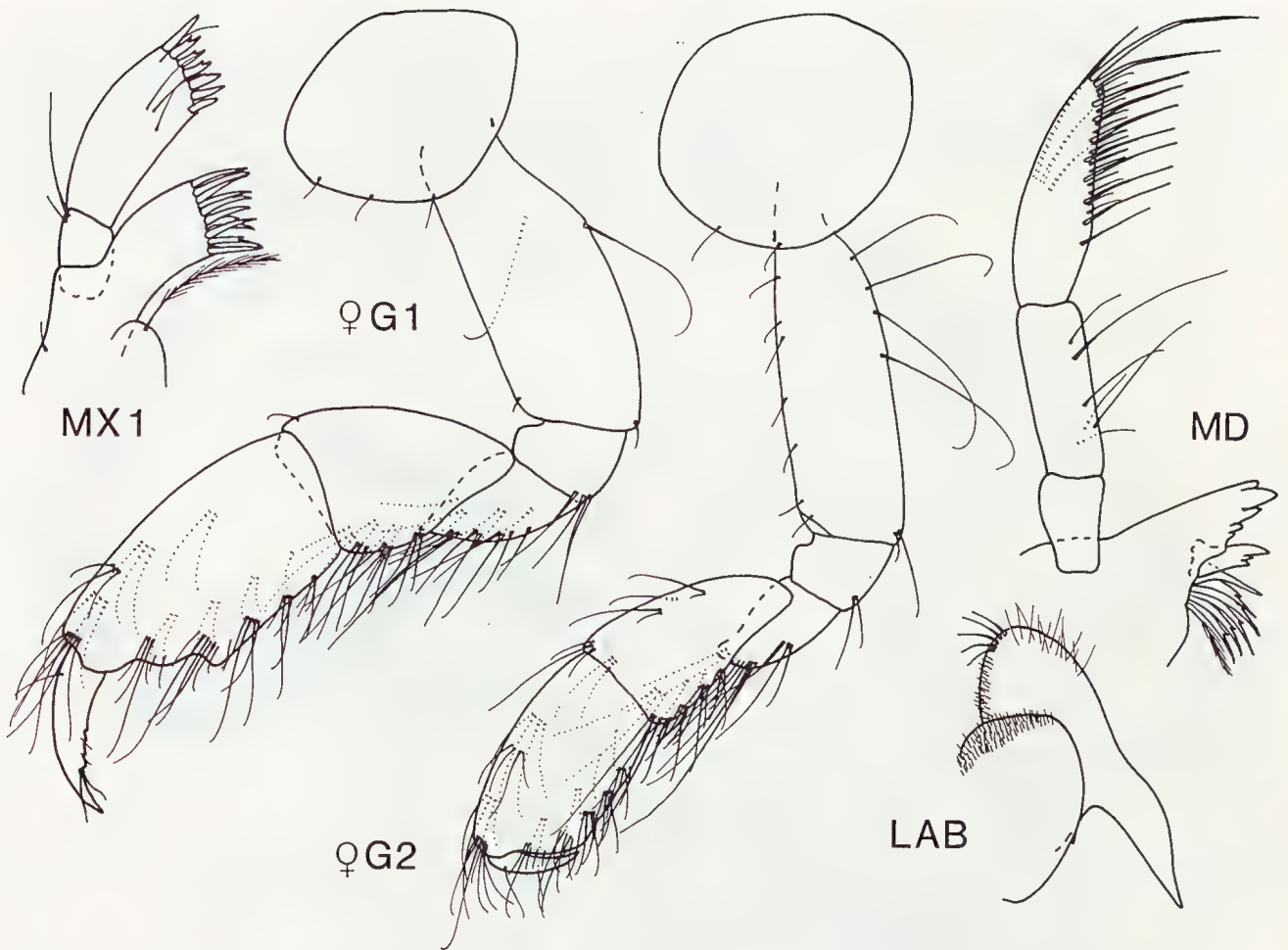


Fig.34. *Bemlos strigilis* n.sp., male, female, Rottneest Island.

***Bemlos arkoolus* n.sp.**

Figs 35–39

Type material. HOLOTYPE: male, 8.0 mm, East of Grassy Creek, Vic., among *Galeolaria* tubes, 23 Jan 1968, W. Seed. NMV J14032. PARATYPES: 1 male, 2 females, type locality, 2 immature, NMV J13708. PARATYPES: 1 male + 1 slide, AM P38615, 1 female + 3 slides, AM P37435, 1 female AM P38616 male, 1 slide female. Stokes Bay, Kangaroo Island, SA, algae at low tide, 4 Mar 1978, L.K. Handley.

Description. (Victoria material). Body (in alcohol) with irregular bands of reddish-brown pigment on head, and pereon segments 2–7, the pigment extending onto the posterior coxae and onto epimera 1–2. Male pereon segments lacking sternal processes. Head anteroventral margin weakly produced, but acute. Labium outer plate distal margin with 2 distal spine-setae. Mandible palp article ratios 3 : 5 : 7, article 3 posterior margin weakly convex with setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Antenna 1 missing. Antenna 2 slender, peduncular article 5 distinctly longer than article 4; flagellum subequal with peduncular article 5, with 12

articles. Male gnathopod 1 coxa anterodistal margin produced, angular, subacute; basis robust, anterior margin substraight, outer face with large wing-like process, curving evenly forward narrowing, but truncate distally; carpus moderate, subtriangular, the posterodistal margin produced into a small, rounded tooth; propodus elongate, twice length of carpus, palm short, oblique, separated from stong, triangular defining tooth by a moderately deep, round-bottomed excavation; tooth with strong proximal spine; dactylus stout, overlapping tooth. Female gnathopod 1 coxa anteriorly rounded; basis moderately stout, lacking process on outer face; carpus subtriangular with posterodistal tooth; propodus elongate, palm sinuous, very oblique; dactylus overlapping palm. Male gnathopod 2 basis stout, anterior margin with proximal fold; carpus very elongate over twice as long as broad; propodus about three quarters length of carpus, palm very oblique; dactylus fitting palm; anterior margin of propodus and anterodistal margin of carpus densely setose. Female gnathopod 2 carpus stout, subtriangular; propodus slightly exceeding length of



Fig.35. *Bemlos arkoolus* n.sp., male, Grassy Creek.

carpus; dactylus fitting palm. Pereopods 3-4 dactylus short, less than half length of propodus. Pereopods 5-7 in the length ratios 3 : 4 : 4. Pereopod 7 a little over one third body length. Epimera 1-3 rounded, but each with a small distoventral depression bearing a small seta. Uropod 1 peduncle with inter-ramal tooth over half length of peduncle;

inner ramus a little longer than outer and a little longer than peduncle. Uropod 2 peduncle with inter-ramal tooth over three quarters length of peduncle; inner ramus longer than outer and longer than peduncle. Uropod 3 rami shorter than peduncle, and lacking marginal spines; outer ramus with small second article.

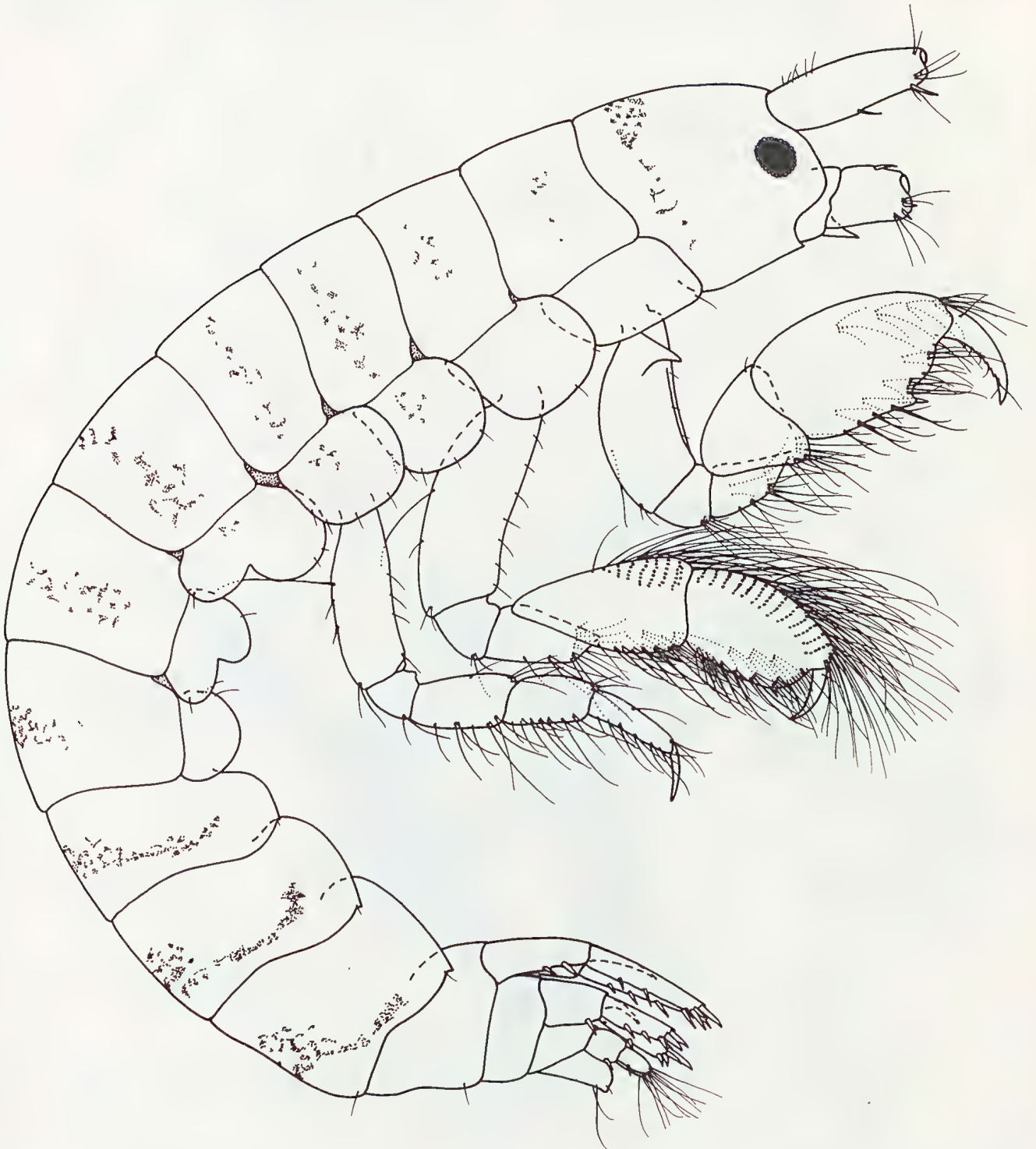


Fig.36. *Bemlos arkoolus* n.sp., male, Stokes Bay.

South Australian material. Body (in alcohol) with head, pereon and pleon segments speckled with red-brown pigment spots which extend on to coxae and epimera. Male gnathopod 1 basis with wing-like process proximal in position; palmar tooth poorly developed. Male gnathopod 2 carpus shorter, only a little longer than propodus.

In both maximum size and in morphological development, this material seems to be submature.

Remarks. This species is readily distinguished by the winged basis of the male gnathopod 1 and elongate setose carpus of the male gnathopod 2. The peculiar folded anterior margin of the basis of the male gnathopod 2 occurs on both left and right

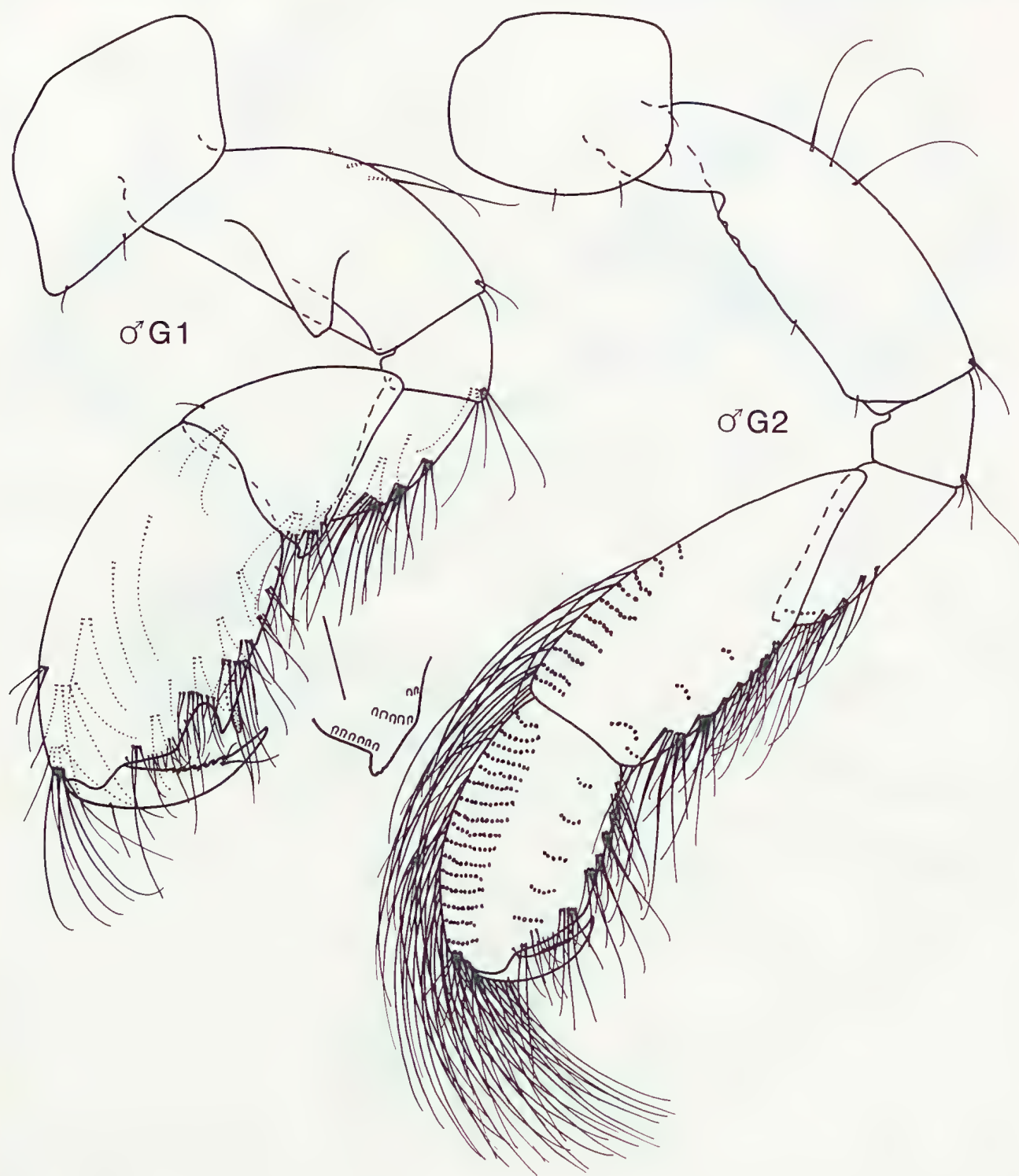


Fig.37. *Bemlos arkoolus* n.sp., male, Grassy Creek.

gnathopods of the only hyperadult male in the collection. It is assumed to be a real character and not a postmortem effect, as the posterior margin is not folded and the folding is similar in both gnathopods.

In the short, stout uropod 3 rami and subovoid mandible palp article 3, this species resembles *Australomicrodeutopus* but differs in the unmodified uropod 1 and unenlarged carpus of the male gnathopod 1. In addition, species of

Australomicrodeutopus lack an inter-ramal process on uropod 2. For the present this species is assigned to *Bemlos*.

Habitat. Among algae and *Galeolaria* in shallow water.

Distribution. Victoria and South Australia.

Etymology. Latinised aboriginal.

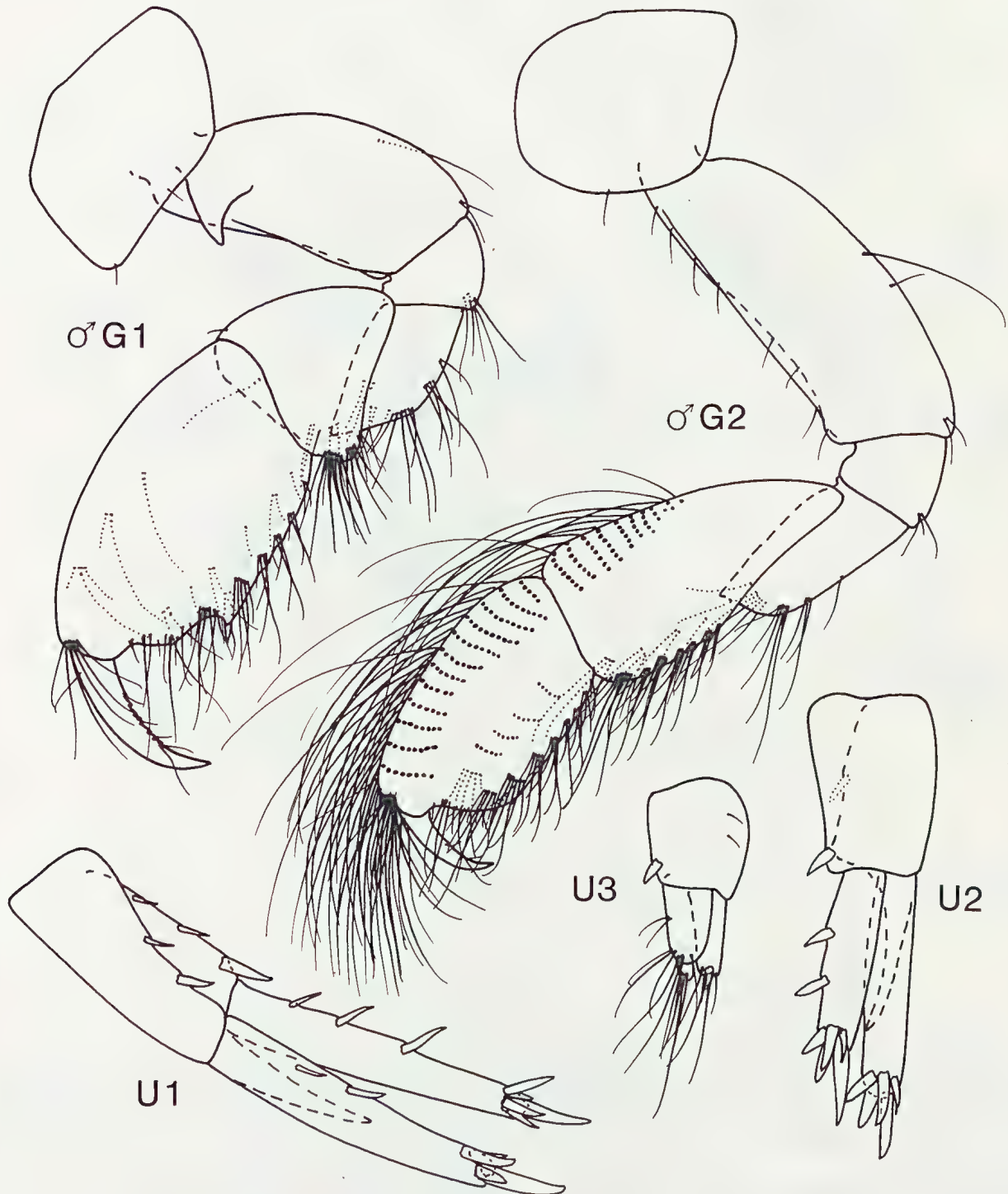


Fig.38. *Bemlos arkoolus* n.sp., male, Stokes Bay.

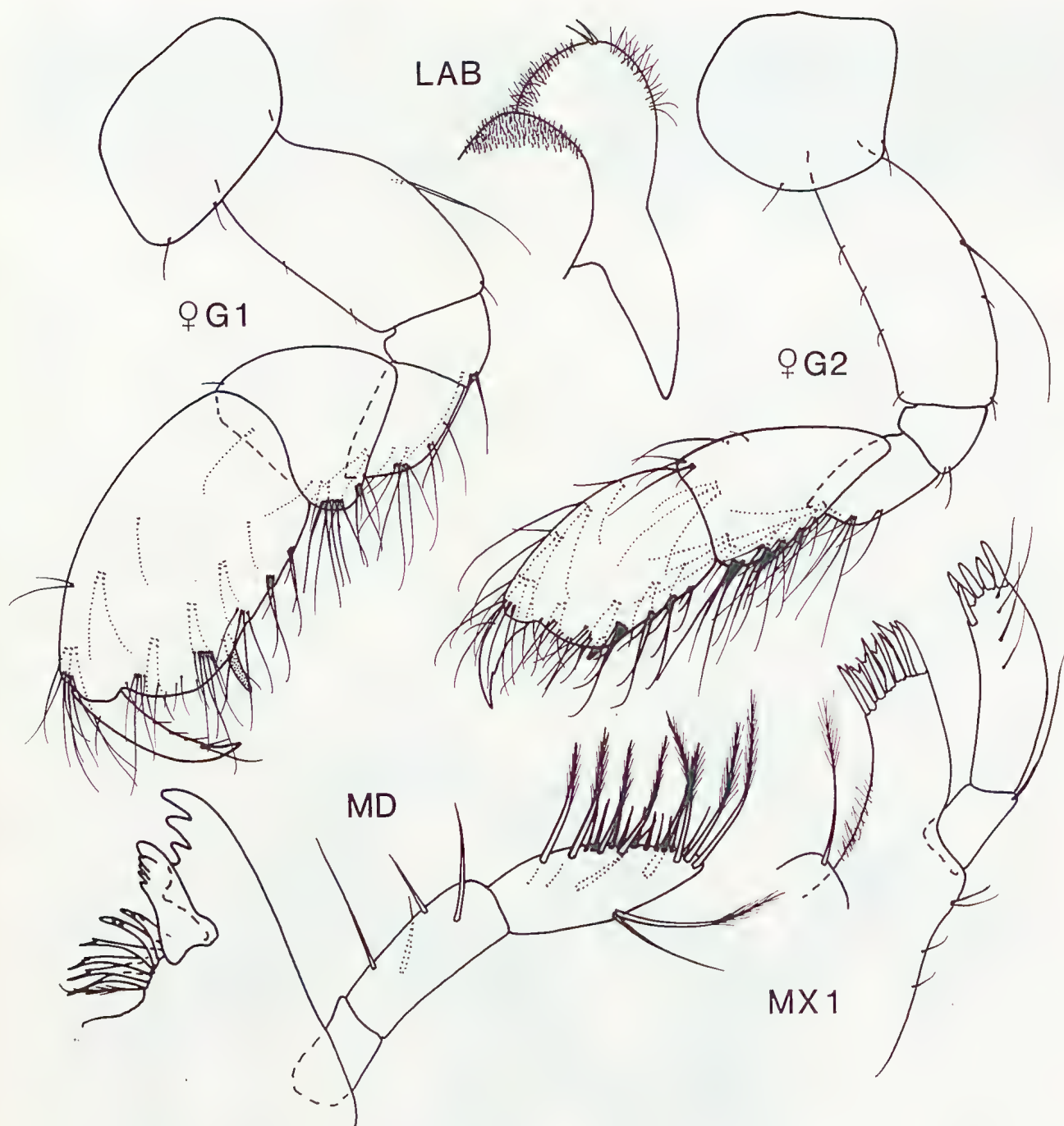


Fig.39. *Bemlos arkooolus* n.sp., male, female, Stokes Bay.

***Bemlos gilgi* n.sp.**

Figs 40-41

Type material. HOLOTYPE: male, 6.2 mm. Shelf, eastern Bass Strait (Victorian Institute of Marine Sciences Cruise 79-k-1, HMAS *Kimbla* Stn 32), 39°41.7'S 148°39.5'E, muddy sand, 115 m, 27 Mar 1979, G.C.B. Poore. NMV J14034. PARATYPES: 22 males, 26 females, + 4 slides, type locality, NMV J13704.

Additional material. 4 males, 1 female. Shelf, eastern Bass Strait (HMAS *Kimbla* Stn 38), 39°22.4' . 148°35.5'E,

muddy sand, 73 m, 29 Mar 1979, G.C.B. Poore, NMV J13703.

Description. Body (in alcohol) uniform pale cream. Male pereon segments without sternal processes. Head anteroventral margin moderately produced. Labium outer plate distal margin with 4 spines. Mandible palp article ratios 1 : 2 : 3, article 3 posterior margin straight, setiferous over three quarters its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 6 distal spines.

Antenna 1 and 2 missing. Male gnathopod 1 weakly setiferous, coxa subquadrangular anterior margin straight, anterodistal margin a little produced; basis stout, anterior margin straight; carpus small, cup shaped; propodus enlarged, over twice length of

carpus anterior margin evenly convex, posterior proximal margin straight, palm short, oblique, posterior margin-palm junction obliterated by long shallow excavation with a spine at its proximal base; dactylus relatively long, opposable to spine. Female

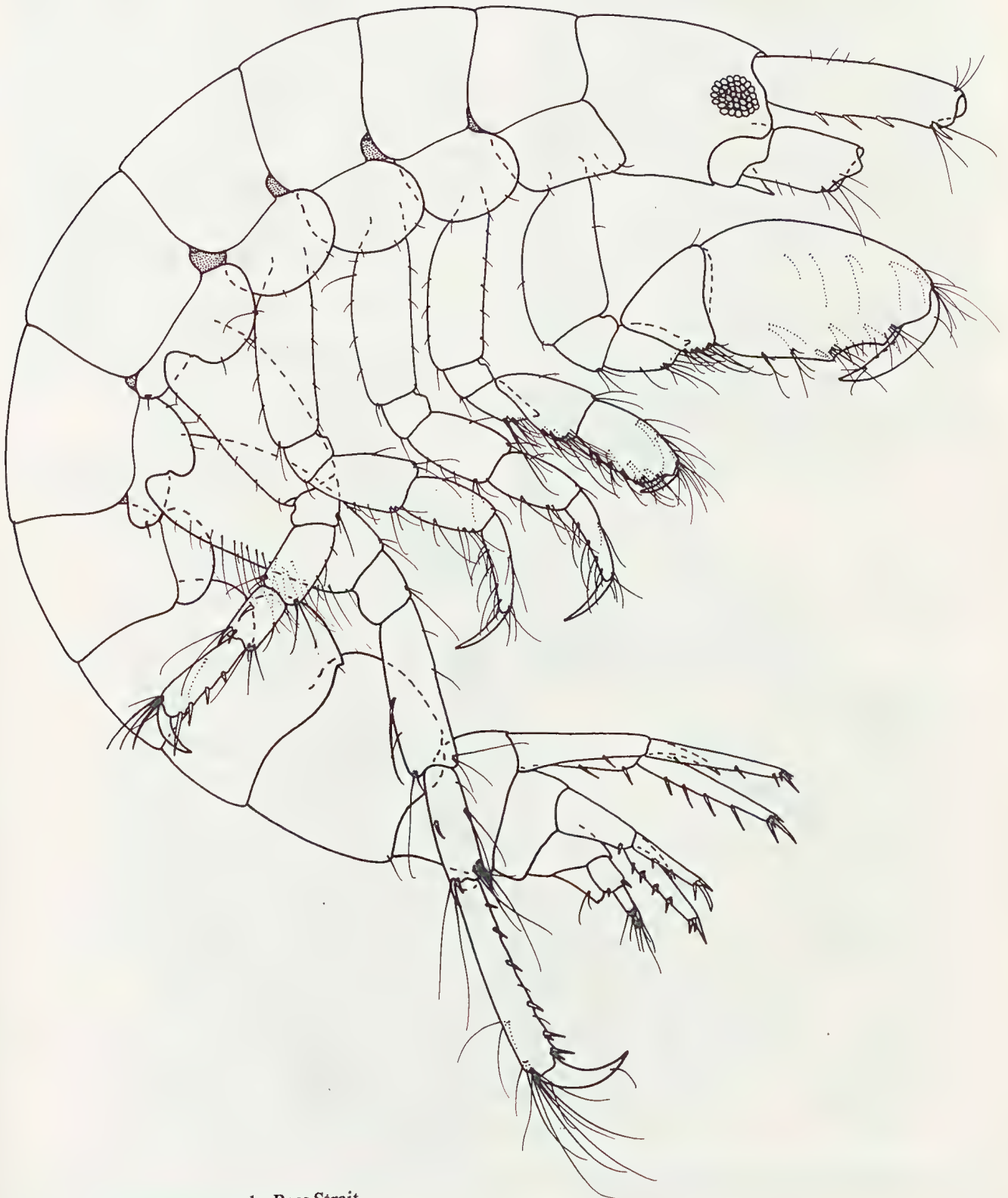


Fig.40. *Bemlos gilgi* n.sp., male, Bass Strait.

gnathopod 1 basis only moderately stout; carpus about one and one half times as long as broad; propodus one and one half times length of carpus, subovoid, palm very oblique, evenly continuous with posterior margin but delimited by spine; dactylus

relatively long, opposable to spine. Male gnathopod 2 basis anterior margin straight, posterior margin moderately convex; carpus only a little shorter than propodus; propodus widest medially, palm oblique; dactylus fitting palm. Female gnathopod 2 not

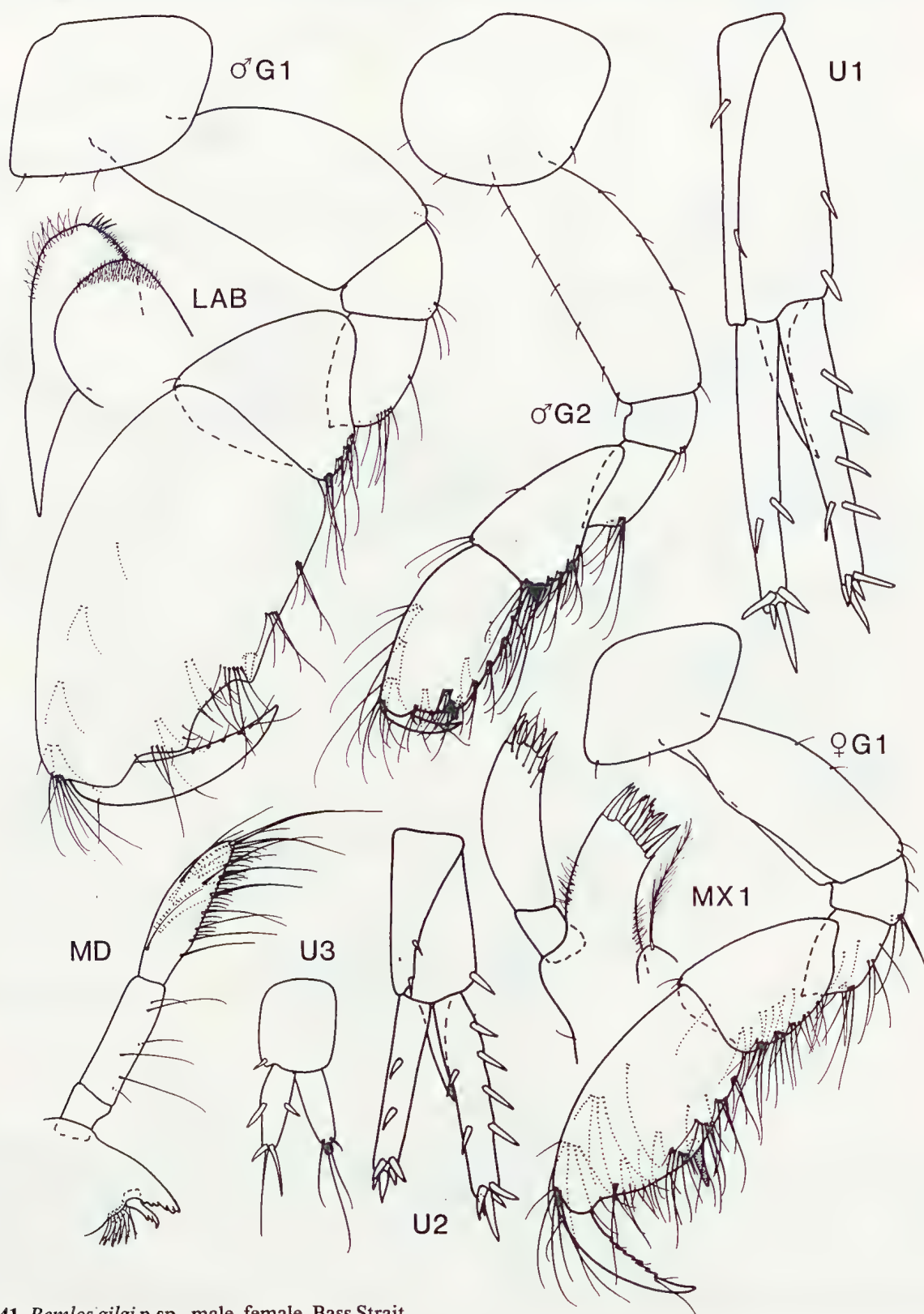


Fig.41. *Bemlos gilgi* n.sp., male, female, Bass Strait.

significantly different from that of male. Pereopods 3 and 4 dactylus two thirds length of propodus. Pereopods 5 and 6 in the length ratio 3 : 5, pereopod 7 missing. Epimera 1–3 with small posterodistal tooth. Uropod 1 peduncle with inter-ramal tooth, half length of peduncle; rami subequal with each other and with peduncle. Uropod 2 peduncle with inter-ramal tooth two thirds length of peduncle; inner ramus longer than outer and longer than peduncle. Uropod 3 rami subequal shorter than peduncle; inner ramus with marginal spines; outer ramus lacking marginal spines or setae, but with small second article bearing long setae.

Remarks. The shape of male gnathopod 1 distinguishes this species from all other known Australian *Bemlos*, but is superficially similar to *Globosolembos excavatus* and *G. lunatus*. However, both of those species have a strongly setose male gnathopod 2.

Habitat. 73–115 m over muddy sand.

Distribution. Bass Strait.

Etymology. Latinised aboriginal.

Protolembos Myers

Protolembos Myers, 1988: 190.

Type species. *Lembos chiltoni* Myers, 1981.

Included species. *P. murrarum* n.sp., *P. drummondiae* n.sp., *P. yarranus* n.sp., *P. arinyas* n.sp., *P. kidoli* (Myers), *P. clematis* (Moore), *P. verrucularum* (Moore).

Diagnosis. Mandible palp article 2 shorter than, but more than two thirds length of article 3, moderately to strongly setiferous, article 3 falcate, elongate, marginal setae variable but with understory of short setae, left molar with rounded plates. Maxilla 1 outer plate with 10 spines. Maxilliped basis with strong flange on anterior margin. Male pereon always lacking sternal processes. Gnathopod 1 enlarged in male, sexually dimorphic. Gnathopod 2 of similar size in both sexes. but sexually dimorphic. Female palm always sinuous. Pereopods 5 and 6 propodus posterior margin with several spines. Uropod 3 inner ramus spinous, outer ramus with small second article and with marginal setae \pm spines.

Remarks. *Protolembos* resembles other plesiomorphic genera such as *Archaeobemlos* and *Arctolembos* but differs from both in the rounded molar plates and flanged maxilliped basis. In addition, it differs from the former in the sexually dimorphic gnathopoda and in lacking a setal row on the anterodistal margin of maxilla palp article 2, and from the latter in the unmodified head lobes, normal labium and unelongate maxilliped palp.

Key to male *Protolembos*

1. Gnathopod 2 propodus short, palm excavate, forming a flat platform (Fig. 46)
..... *P. drummondiae*
- Gnathopod 2 propodus elongate, palm variable, but never as above 2
2. Gnathopod 1 with palmar defining tooth and with medial tooth on posterior margin 3
- Gnathopod 1 with palmar defining tooth only 4
3. Gnathopod 2 propodus with acute palmar tooth (*P. kidoli*)
- Gnathopod 2 propodus lacking palmar tooth *P. murrarum*
4. Pereon segments 1–4 with sternal processes *P. clematis*
- Pereon segments lacking sternal processes 5
5. Gnathopod 1 basis, ischium and merus with long setae 6
- Gnathopod 1 basis, ischium and merus with short setae only *P. verrucularum*
6. Gnathopod 2 carpus and propodus anterior margin with dense clothing of long setae, propodus palm without defining tooth 7
- Gnathopod 2 carpus and propodus anterior margin only moderately setiferous, propodus with short defining tooth *P. chiltoni*
7. Gnathopod 1 carpus anterior margin with dense brush of long setae *P. arinyas*
- Gnathopod 1 carpus anterior margin with dense brush of short setae *P. yarranus*

Only one species of *Protolembos* is known from outside Australian waters, it is included in the above key in parentheses.

***Protolembos chiltoni* (Myers)**

Lembos chiltoni Myers, 1981: 104, figs 216–219.
Protolembos chiltoni Myers, 1988: 191.

Material examined. Tasmania: HOLOTYPE: 1 male, D'Entrecasteaux Channel, Hobart, east of Middleton, euhaline, 5 Oct 1973, T.M. Walker, AM P37850. PARATYPES: 1 female, type locality, AM P37851; 1 male,

D'Entrecasteaux Channel, 200 m offshore of Gallagher's Point, in *Heterozostera tasmanica*, euhaline, 11 Apr 1975, T.M. Walker; 3 females, D'Entrecasteaux Channel, 200 m east of Kettering Point, 11 Apr, 1975, T.M. Walker. Victoria: 2 males, 7 females, Crib Point, Westernport, 38°21.65'S 145°15.21'E, 2 m, sandy mud, 13 Apr 1965, NMV J14040.



Fig.42. *Protolembos murrarum* n.sp., male, Jervis Bay.

Remarks. This material was fully figured by Myers (1981).

Habitat. Presumed to be phanerogammes and algae.

Distribution. Tasmania and Victoria.

Protolembos murrarum n.sp.

Figs 42–44

Type material. HOLOTYPE: male, 5.0 mm. Off Plantation Point, Jervis Bay, NSW, weed, 21 Feb 1982, P.B. Berents, AM P37436. PARATYPES: 2 males, 4 females, + 7 slides, type locality, AM P37437.

Additional material. 2 males, 3 females, off Plantation Point, Jervis Bay, NSW, *Liagora* washings, 3 m, 25 Sept

1982, P.B. Berents, AM P37438; 3 females, near Moona Moona Creek, Jervis Bay, NSW, with ascidians, 5 m, 18 June 1982, P.B. Berents, AM P37439.

Description. Body (in alcohol) irregularly and strongly mottled with dark brown pigment which extends onto coxae, epimera, pereopod bases and uropod peduncles. Male pereon segments without sternal processes. Head anteroventral margin moderately produced, acute; eye large. Labium outer plate distal margin with about 8 spines. Mandible palp article ratios 2 : 5 : 6, article 3 posterior margin weakly concave and setiferous over two thirds of its length, marginal setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Antenna 1 missing in all specimens. Antenna 2 peduncular article 4

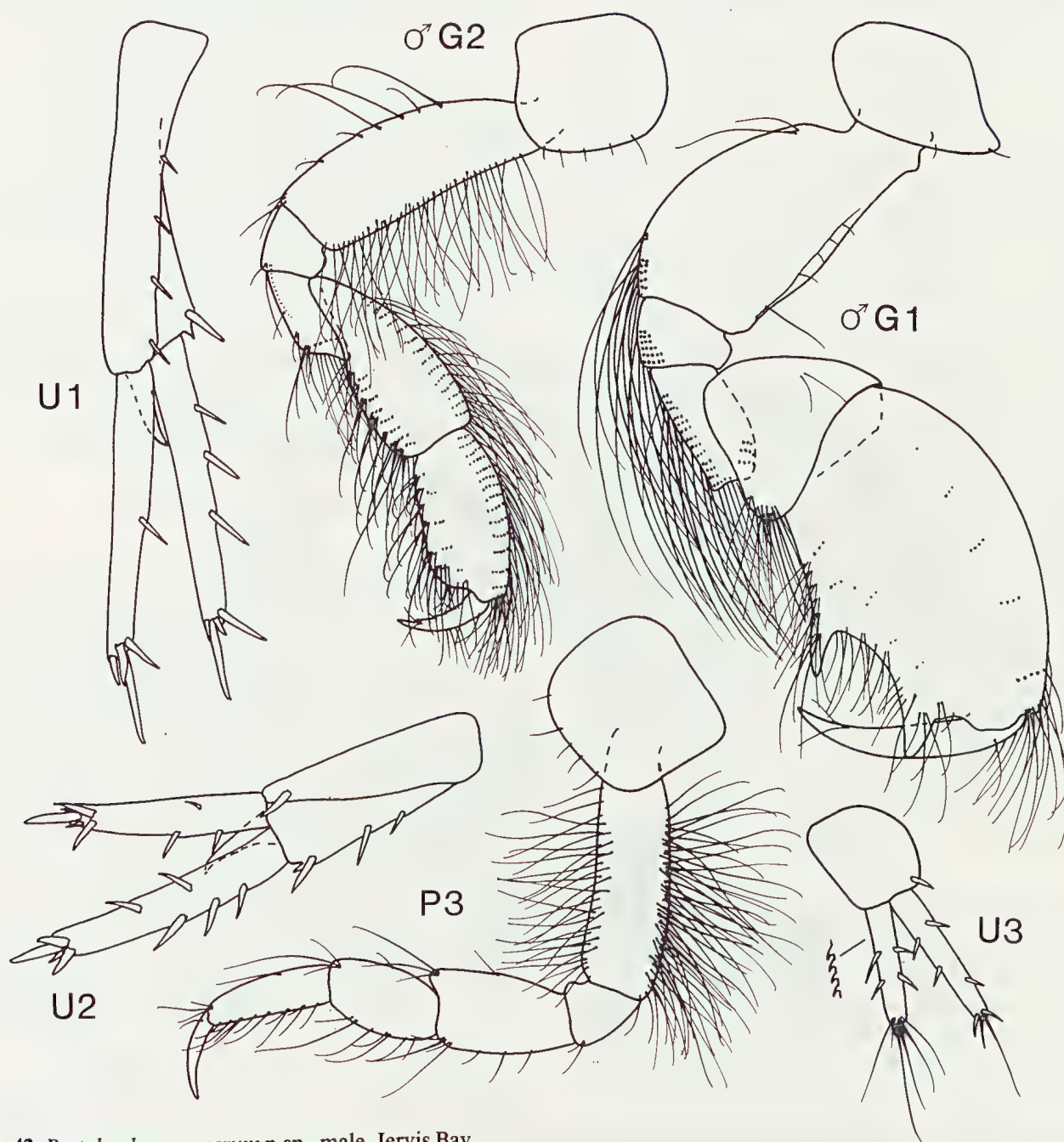


Fig.43. *Protolembos murrarum* n.sp., male, Jervis Bay.

slightly longer than article 5; flagellum slender, a little longer than peduncular articles 5 with about 7 articles. Male gnathopod 1 coxa anterodistal margin produced, rounded; basis swollen, anterior margin irregularly convex; basis, ischium and merus posterior margins each with a brush of very long setae; merus subrectangular; carpus short, cup shaped; propodus two and one half times length of carpus, posterior margin with a strong medial and a strong distal tooth separated by a concave excavation, palm short, delimited by distal tooth;

dactylus elongate, greatly overlapping palm and opposable to medial tooth. Female gnathopod 1 carpus subovoid; propodus distinctly longer than carpus, palm oblique, defined by a rounded tooth, proximal to which is a spine; dactylus overlapping palm. Male gnathopod 2 basis anterior margin straight, heavily setose; carpus and propodus slender; carpus the longer, both podomeres with heavily setose anterior and posterior margins, palm oblique; dactylus overlapping palm. Female gnathopod 2 propodus distinctly longer than carpus;

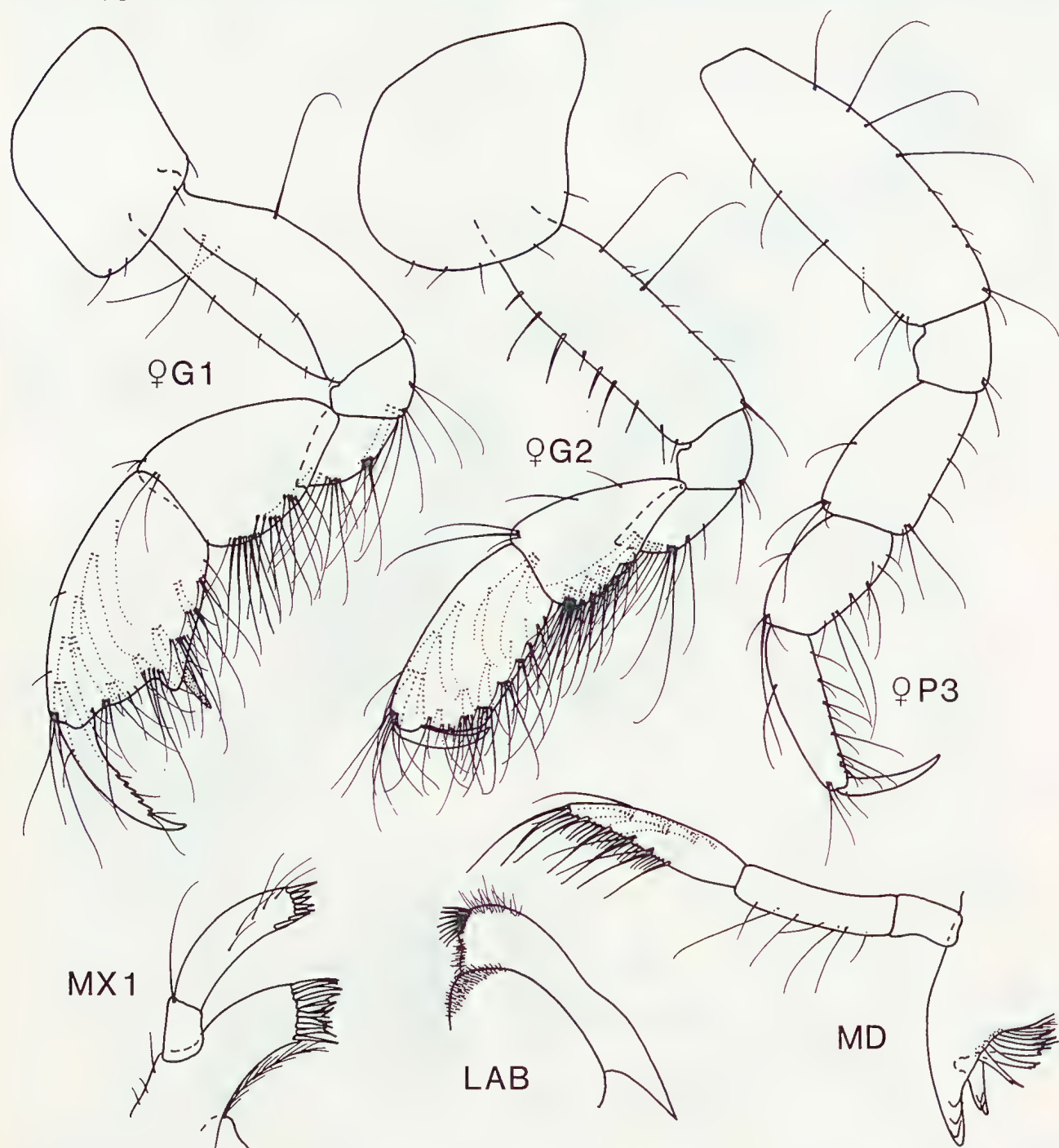


Fig.44. *Protolembos murrarum* n.sp., male, female, Jervis Bay.

anterior margins of basis, carpus and propodus only moderately setiferous, palm oblique; dactylus fitting palm. Male pereopod 3–4 basis heavily setose on anterior and posterior margins; dactylus two thirds length of propodus. Female pereopods 3–4 basis weakly setiferous. Pereopods 5–7 in the length ratios 2 : 3 : 4; pereopod 7 less than two thirds body length. Epimera 1–3 with small posterodistal tooth. Uropod 1 peduncle with inter-ramal process less than one quarter length of peduncle; rami subequal and shorter than peduncle. Uropod 2 peduncle with inter-ramal process over one third length of peduncle; inner ramus stouter and longer than outer ramus and longer than peduncle. Uropod 3 rami slender, margins minutely denticulate; inner ramus longer than outer and one and one half times length of peduncle; outer ramus with small second article and very long terminal setae.

Remarks. This species is closely related to *P. kidoli* (Myers). It differs in the more linear basis and simple palm of the male gnathopod 2, in the presence of setal brushes on the basis, ischium and merus of the male gnathopod 1, in the setose basis of the male pereopods 3 and 4 and in the shorter pereopod 7 as well as in the shape and chaetotaxy of the mandible palp. The minute denticulation of the margins of the uropod 3 rami appears to be unique to these two species. It also resembles *P. drummondiae*. For differences see remarks under that species.

Habitat. Among algae and epizooites in shallow water.

Distribution. Known only from the type locality.

Etymology. Latinised aboriginal.

***Protolembos drummondiae* n.sp.**

Figs 45–47

Type material. HOLOTYPE: male, 10.0 mm. Westernport, Vic., 38°21.30'S 145°22.83'E, 6m, 26 Nov 1973, NMV J14038. PARATYPES: 3 males, 3 females, + 6 slides, type locality, NMV J13644.

Additional material. Westernport, Victoria: 1 male, 1 female, 38°14.47'S 145°21.86'E, mud, intertidal, 7 Jan 1974, NMV J13691; 5 males, 3 females, 38°15.31'S 145°22.38'E, sandy-clay, intertidal, 8 Jan 1974, NMV J13643; 6 males, 1 female, 38°18.56'S 145°22.52'E, sand, intertidal, 9 Jan 1974, NMV J13640; 1 female, 38°16.12'S 145°24.52'E, sand, 12 m, 9 Jan 1974, NMV J13645; 1 female, 38°28.81'S 145°25.10'E, clayey-sand, intertidal, 24 Jan 1974, NMV J13638; 1 male, 1 female, 38°22.90'S 145°31.83'E, sand-silt-clay, intertidal, 24 Jan 1974, NMV J13642; 2 males, 2 females, 38°21.65'S 145°31.69'E, intertidal, 29 Jan 1974, NMV J13639; 1 female, 38°27.53'S 145°08.59'E, sand, 18 m, 25 Nov 1974, NMV J13637. Crib Point, Victoria: 1 female, 38°19.95'S 145°15.13'E, mud and *Zostera*, 2 m, 16 Mar 1965, NMV J13787.

Description. Body (in alcohol) uniformly but irregularly mottled in dark brown, head with reticulate pattern. Male pereon segments without sternal processes. Head anteroventral margin

unproduced. Labium outer plate distal margin with about 10 spines. Mandible palp article ratios 3 : 7 : 8, article 3 elongate, falcate, posterior margin with setae of 2 distinct lengths. Maxilla 1 palp article 2 with 7 distal spines. Maxilliped basis with flange on anterior margin, ischium with small protrusion on anterior margin. Antenna 1 missing. Antenna 2 peduncular article 4 with large ventral flange, broader proximally than distally; article 5 slender, but subequal in length with peduncular article 4; flagellum subequal with peduncular article 5, with about 12 articles. Male gnathopod 1 coxa subquadrangular, anterior margin straight or weakly concave, not markedly produced; basis only moderately broad, anterior distal margin produced into a small rounded tooth; carpus short cup shaped; propodus enlarged, three and one half times length of carpus, palm short, transverse, separated from long, slender, acute tooth by a deep, triangular, round bottomed excavation; posterior margin of ischium, carpus and propodus densely setose, anterior margin of carpus and propodus weakly setiferous; dactylus slender, elongate, greatly overlapping palm. Female gnathopod 1 carpus three quarters length of propodus; palm of propodus oblique, sinuous; dactylus slender, overlapping palm. Male gnathopod 2 basis anterior margin sinuous, minutely crenulate, posterior margin weakly convex; carpus stout; propodus broader but shorter than carpus, true palm obsolete, replaced by straight, subdistal shelf, delimited by a spine; posterior margin of ischium, carpus and propodus and distal margin of propodus densely setose; dactylus slender, fitting false palm. Female gnathopod 2 basis slender; carpus and propodus slender, subequal, palm oblique, evenly convex; dactylus fitting palm. Pereopods 3 and 4 dactylus about half length of propodus. Pereopods 5 and 6 in the length ratio 2 : 3. Pereopod 7 missing. Epimera 1–3 each with a distoventral tooth. Uropod 1 peduncle with inter-ramal tooth one third length of peduncle; rami slender, subequal, longer than peduncle. Uropod 2 peduncle with inter-ramal tooth more than one third length of peduncle; rami slender; inner ramus longer than outer and longer than peduncle. Uropod 3 rami elongate; inner ramus with marginal spines; outer ramus with spines on inner margin and setae on outer margin and with small second article; both rami with long terminal setae; inner ramus over one and one half times length of peduncle.

Remarks. This species appears to be most closely related to *P. murrarum*, but differs in the peculiarly flanged article 4 of the male antenna 2, in the excavated palm of the male gnathopod 2, in the poorly setiferous basis of the male pereopods 3 and 4, in the flanged basis of the maxilliped and in the longer uropod 3 rami. It also resembles *P. kidoli* from East Africa but in that species the tooth on the propodus of the male gnathopod 1 is more proximal and the entire appendage less setose and male



Fig.45. *Protolembos drummondiae* n.sp. male, Westernport.

gnathopod 2 has a flask-shaped basis, strongly setose anterior margin to the carpus and slender propodus with an acute posterodistal tooth.

Habitat. On muds and sands, sometimes with *Zostera* from the intertidal to 18 m depth.

Distribution. Known only from Victoria.

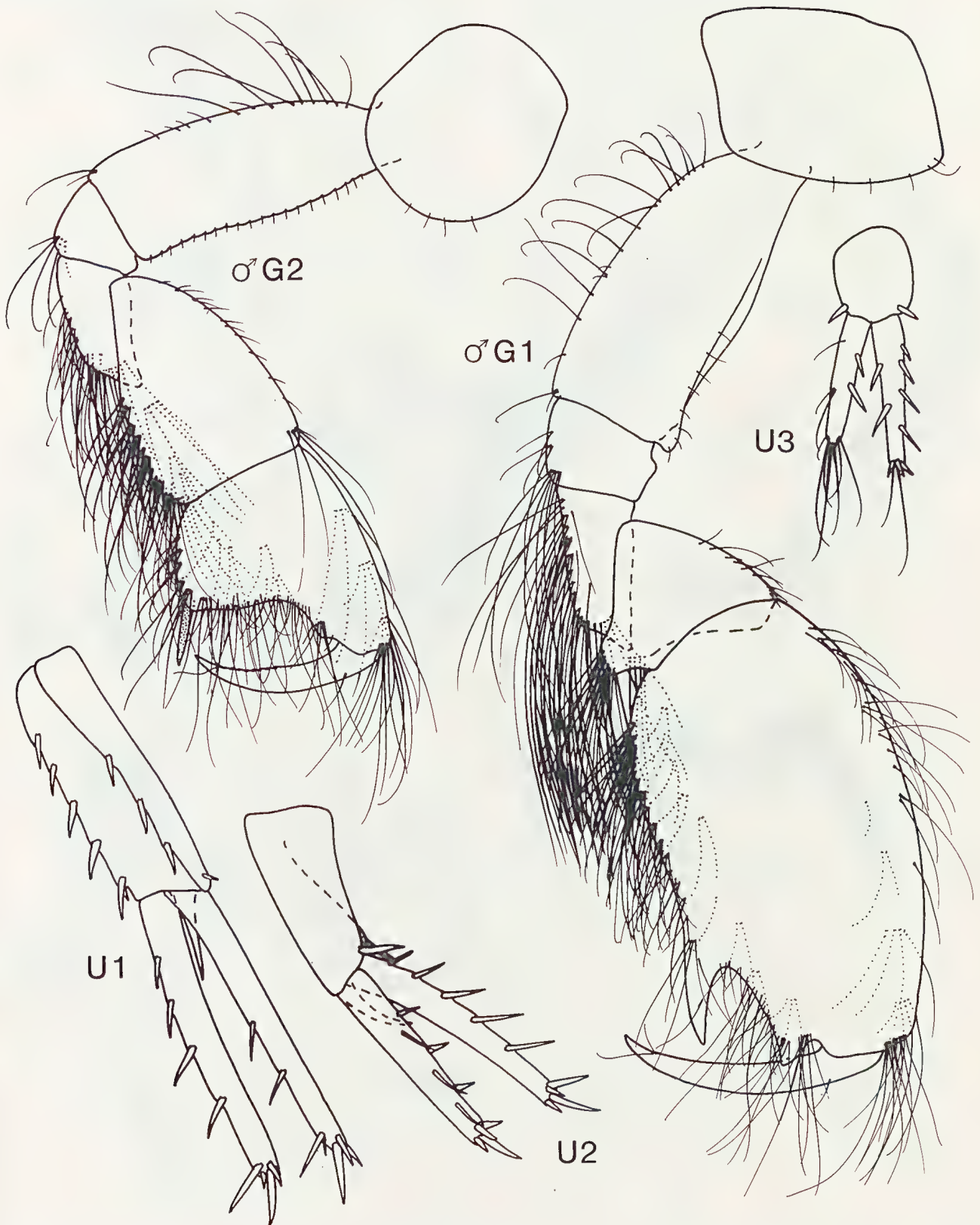


Fig.46. *Protolembos drummondiae* n.sp. male, Westernport.

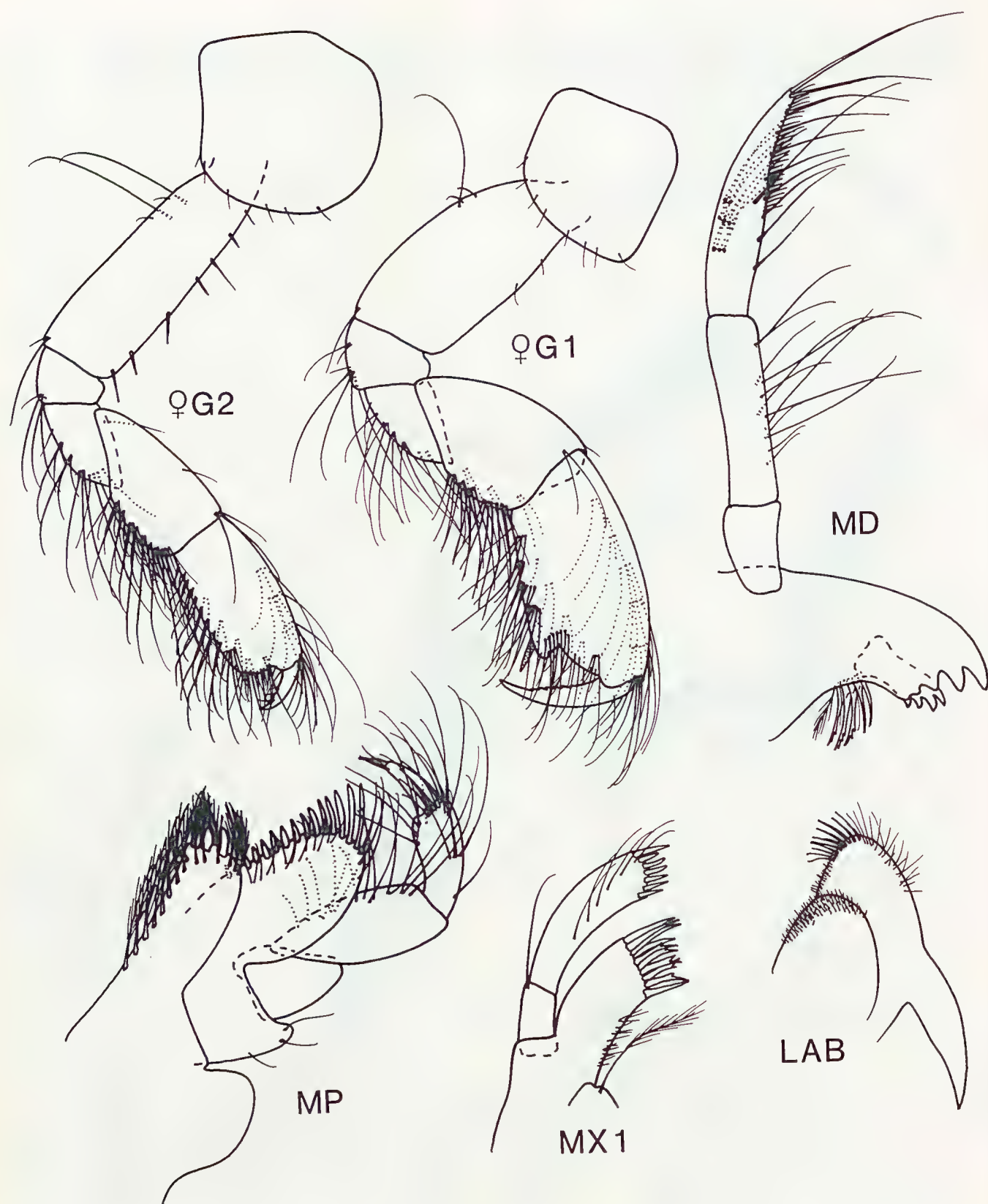


Fig.47. *Protolembos drummondiae* n.sp. female, Westernport.

Etymology. In honour of Margaret M. Drummond, Museum of Victoria, for her fine works on Australian Amphipoda.

***Protolembos clematis* (Moore)**

Lembos clematis Moore, 1987: 778, fig. 3.

Remarks. This species is well figured by Moore (1987).

Habitat. In holdfasts of *Macrocystis pyrifera*.

Distribution. Tasmania.



Fig.48. *Protolembos yaranus* n.sp., male, Kalbarri.

Protolembos yaranus n.sp.

Figs 48–50

Type material. HOLOTYPE: male, 5.2 mm, Red Bluff, Kalbarri, WA, 27°42'S 114°09'E, mixed algae and sediment, 3–4 m, 10 Jan 1984, R.T. Springthorpe, AM P37440. PARATYPES: 4 males + 1 slide, AM P37441, 6 females + 2 slides, AM P38617, type locality.

Additional material. Western Australia. 1 male, Vancouver Peninsula, near Mistaken Island, Albany, 35°04'S 117°56'E, sponges, 2 m, 13 Dec 1983, J.K. Lowry, AMP37442.

Description. Body (in alcohol) with dorsal bands of dark brown pigment on pereon segments 1–7 and pleon segments 1–2. Coxae 1–7 and epimera 1–3 with small central patches of similar pigment. Male

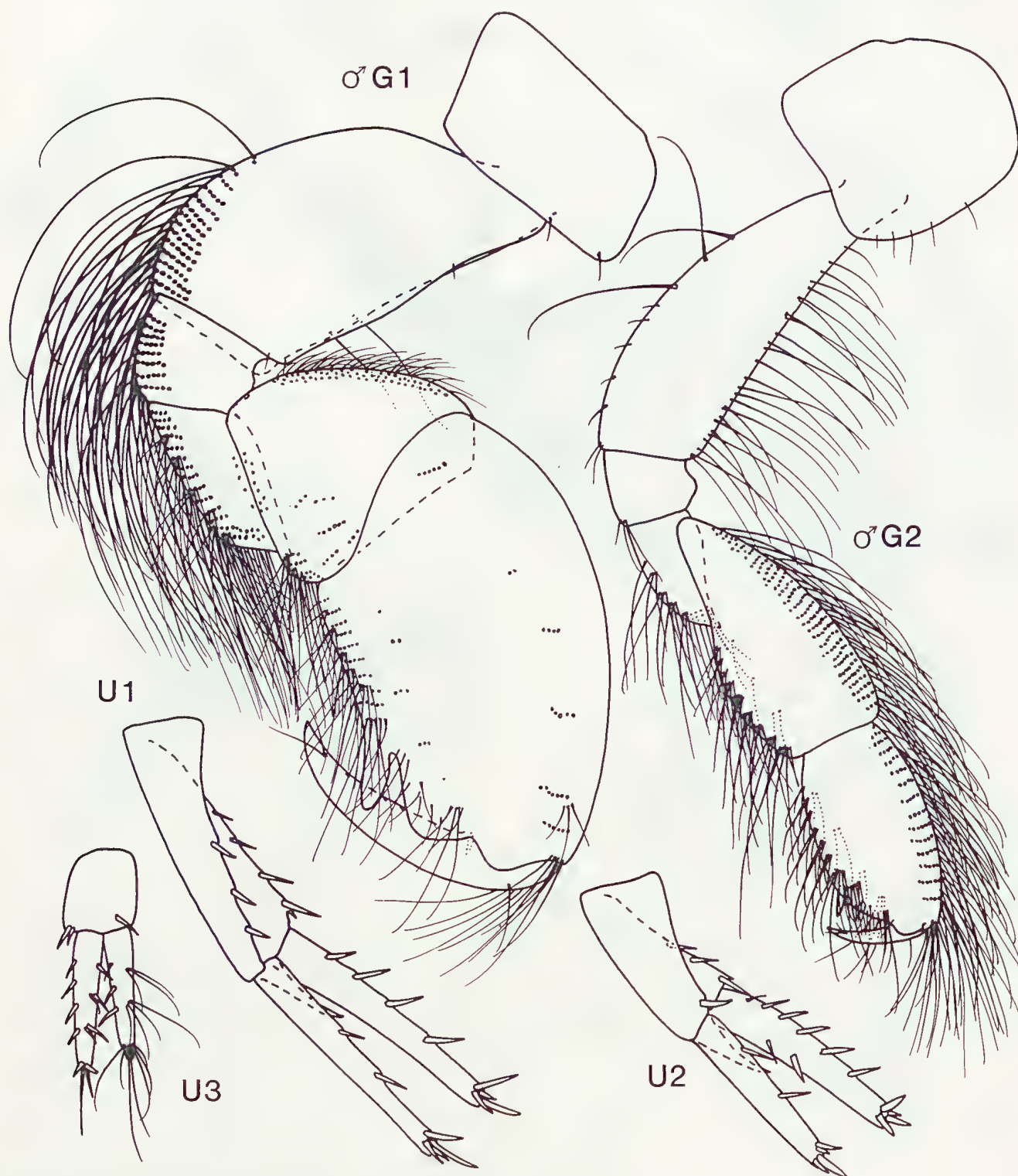


Fig.49. *Protolembos yaranus* n.sp., male, Kalbarri.

pereon segments without sternal processes. Head anteroventral margin unproduced. Labium outer plate distal margin with 8 spines. Mandible palp article ratios 3 : 6 : 8, article 3 elongate, weakly falcate, posterior margin with setae of 2 distinct lengths. Maxilla 1 palp article 2 with 8 distal spines. Maxilliped basis with flange on anterior margin, ischium with small protrusion on anterior margin. Antenna 1 missing. Antenna 2 peduncular articles 4 and 5 subequal in length; flagellum subequal in length with peduncular article 5 with about 9 articles. Male gnathopod 1 coxa subquadrangular, anterior margin straight, anterodistal margin a rounded right angle; basis greatly expanded, anterior margin weakly convex, posterior margin strongly convex; carpus short, cup shaped; propodus over twice length of carpus, broadest medio-proximally, palm short, oblique, separated from thumb-like posterodistal

tooth by deep, narrow, v-shaped excavation; dactylus elongate greatly overlapping posterodistal tooth; posterior proximal margin of basis and posterior margins of ischium and merus with dense brush of long setae, anterior margin of carpus with dense brush of relatively short setae. Female gnathopod 1 basis stout; propodus one and a half times length of carpus, parallel sided, palm sinuous, defined by triangular tooth and a spine; dactylus slender, overlapping tooth. Male gnathopod 2 basis anterior margin straight, with numerous long setae, posterior margin moderately convex; carpus : propodus ratio 5 : 4; propodus subovoid, palm oblique evenly continuous with posterior margin, but delimited by a spine; dactylus slender, scarcely overlapping palm; anterior margin of carpus and propodus densely setose. Female gnathopod 2 carpus and propodus subequal; palm oblique; dactylus fitting palm.

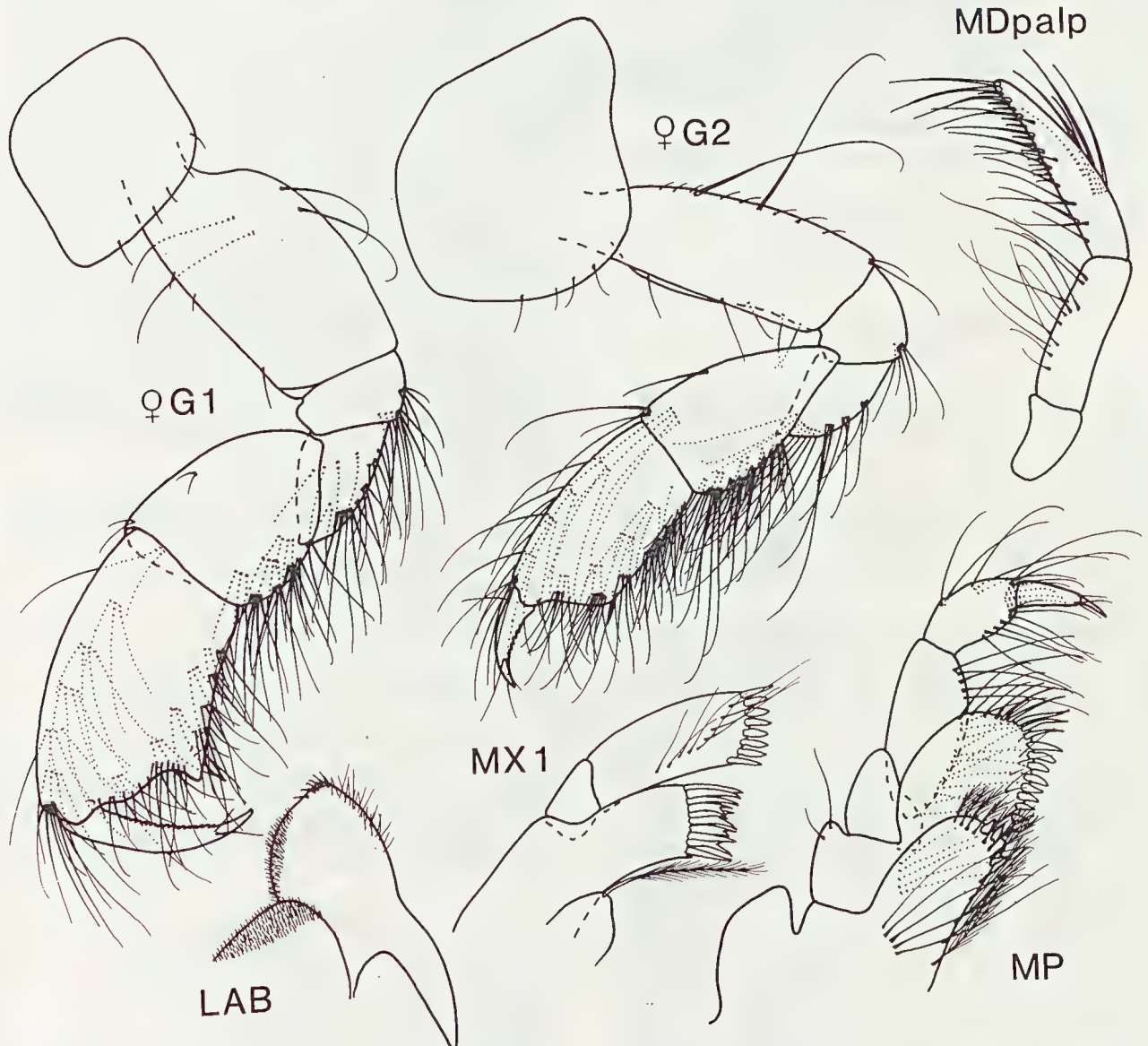


Fig.50. *Protolembos yaranus* n.sp., male, female, Kalbarri.

Pereopods 3 and 4 with anterior margin of basis strongly setose; dactylus half length of propodus. Pereopods 5–7 in the length ratio 4 : 5 : 9; pereopod 7 two thirds body length. Epimera 1–3 each with a distoventral tooth. Uropod 1 peduncle with interramal tooth one third length of peduncle; rami slender, subequal, scarcely shorter than peduncle. Uropod 2 peduncle with interramal tooth less than half length of peduncle; rami stout, inner ramus longer than outer and longer than peduncle. Uropod 3 rami elongate over one and a half times length of peduncle; inner ramus with marginal spines; outer ramus with spines on inner margin and setae on outer margin and with small second article bearing a pair of long setae.

Remarks. *Protolembos yaranus* is a sibling species of *P. arinyas* from Victoria. It differs from the latter species in the more slender antenna 2 with more flagellar articles and in the different male gnathopod 1 in which the palmar tooth is weakly divergent, the relatively short setae on the anterior margin of the carpus, and the sparse setae on the anterior margin of the propodus. In the male gnathopod 2 the palm is evenly convex, not sinuous as in *P. arinyas*.

Habitat. Epifaunal among algae and sponges in 2–4 m.

Distribution. Western Australia.

Etymology. Latinised aboriginal.

Protolembos arinyas n.sp.

Figs 51–53

Type material. HOLOTYPE: male, 8.0 mm, Corner Inlet, Nooramunga, Vic., CIN Station 28E, Nov 1983, NMV J14037. PARATYPES: 2 males, 6 females, + 6 slides, type locality, NMV J12659.

Additional material. Westernport, Vic., 10 males, 16 females, 100 l mm, 38°27.53'S 145°08.59'E, 18 m, sand, 25 Nov 1974, NMV J13666; 4 males, 9 females, 10 l mm, 38°26.48'S 145°13.03'E, 23 m, sand, 25 Nov 1974, NMV J13667.

Description. Body (in alcohol) variably mottled in dark brown over much of the surface of the head, body coxae and antennal and uropod peduncles. Male pereon segments without sternal processes. Head anteroventral margin only moderately produced; eye relatively large. Labium outer plate distal margin with 9 simple spines and a compound coronate spine. Mandible palp article ratios 2 : 6 : 7 article 3 elongate, weakly falcate, posterior margin with setae of 2 distinct lengths. Maxilla 1 palp article 2 with 8 distal spines. Maxilliped basis with flange on anterior margin, ischium with small protrusion on anterior margin. Antenna 1 missing. Antenna 2 peduncular articles 4 and 5 subequal; flagellum shorter than peduncular article 5 with 5 stout articles. Male gnathopod 1 coxa subquadrangular, anterior margin straight, anterodistal margin rounded; basis expanded, flask shaped; carpus short

subtriangular; propodus one and a half times length of carpus, approximately parallel sided, palm short, oblique, separated from strong triangular tooth by a broad, v-shaped excavation; dactylus elongate, slightly overlapping tooth; posterior proximal margin of basis and posterior margins of ischium, merus, carpus and propodus with dense brush of very long setae, anterior margin of carpus and propodus with very long setae in profusion. Female gnathopod 1 basis stout; propodus one and a half times length of carpus, parallel sided, palm sinuous defined by a triangular tooth and a spine; dactylus slender, overlapping tooth. Male gnathopod 2 basis anterior margin straight, with numerous long setae, posterior margin quite strongly convex; carpus : propodus ratio 8 : 7, propodus broadening distally, palm sinuous, distinct from posterior margin and delimited by a spine; dactylus slender, scarcely overlapping palm; anterior margin of carpus and propodus densely setose. Female gnathopod 2 propodus longer than carpus, palm oblique; dactylus fitting palm. Pereopods 3 and 4 with anterior margin of basis strongly setose; dactylus over half length of propodus. Pereopods 5 and 6 in the length ratio 5 : 6; pereopod 7 missing. Epimeron 1 rounded; epimera 2–3 with strong distoventral tooth. Uropod 1 peduncle with inter-ramal tooth one third length of peduncle; rami slender, subequal, slightly longer than peduncle. Uropod 2 peduncle with inter-ramal tooth less than half length of peduncle; inner ramus longer than outer and longer than peduncle. Uropod 3 rami elongate; inner ramus one and a half times length of peduncle with marginal spines; outer ramus with spines on inner margin, setae on outer margin and with small second article bearing a pair of long setae.

Remarks. This species is closely related to *P. yaranus* n.sp. For distinguishing characters see under remarks for that species.

Habitat. On sandy bottoms in ? 18–23 m.

Distribution. Victoria.

Etymology. Latinised aboriginal.

Protolembos verrucularum (Moore)

Lembos verrucularum Moore, 1987: 780, fig. 4.

Remarks. This species is well figured by Moore (1987).

Habitat. In holdfasts of *Macrocystis pyrifera*.

Distribution. Tasmania.

Globosolembos Myers

Globosolembos Myers, 1985a: 341.

Type species. *Autonoe smithi* Holmes.

Included species. See Myers (1985a).

Diagnosis. Mandible palp article 2 shorter than article 3 moderately to strongly setiferous, article 3

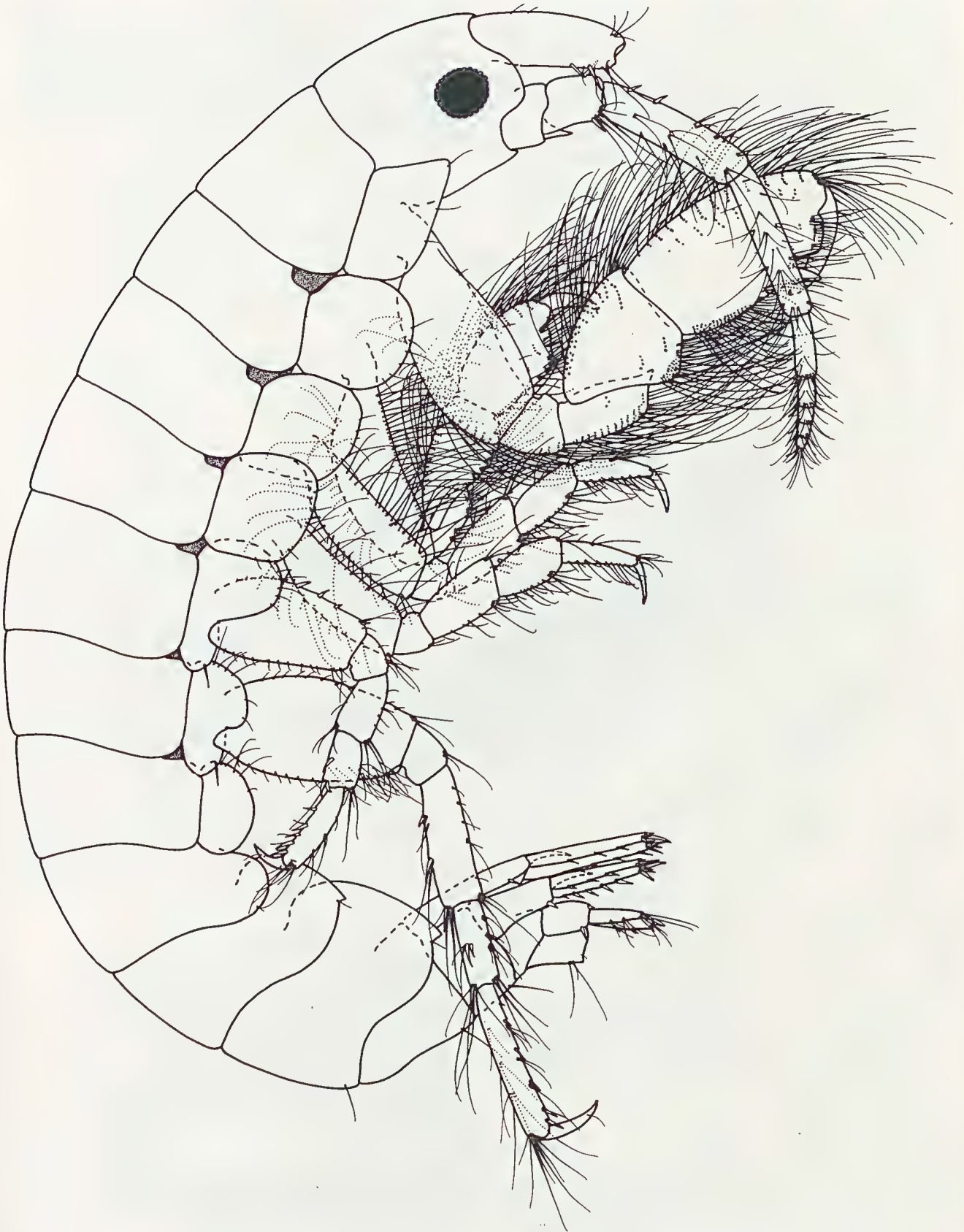


Fig.51. *Protolembos arinyas* n.sp., male, Nooramunga.

generally falcate, elongate, rarely shortened subovoid, marginal setae variable, generally of more than 2 distinct lengths, left molar with well developed plates, the primary plate falcate. Gnathopod 1 equally or almost equally enlarged in both sexes with little sexual dimorphism, propodus larger than carpus tending to globose, lacking an intrapalmar excavation but sometimes with

excavation on palmar-posterior margin, defining process or tooth weak or absent. Gnathopod 2 generally setose in both sexes, sometimes less so in female. Pereopods 5 and 6 propodus posterior margin with setae but never spines, except for palmar locking spine. Uropod 3 outer ramus lacking a second article.

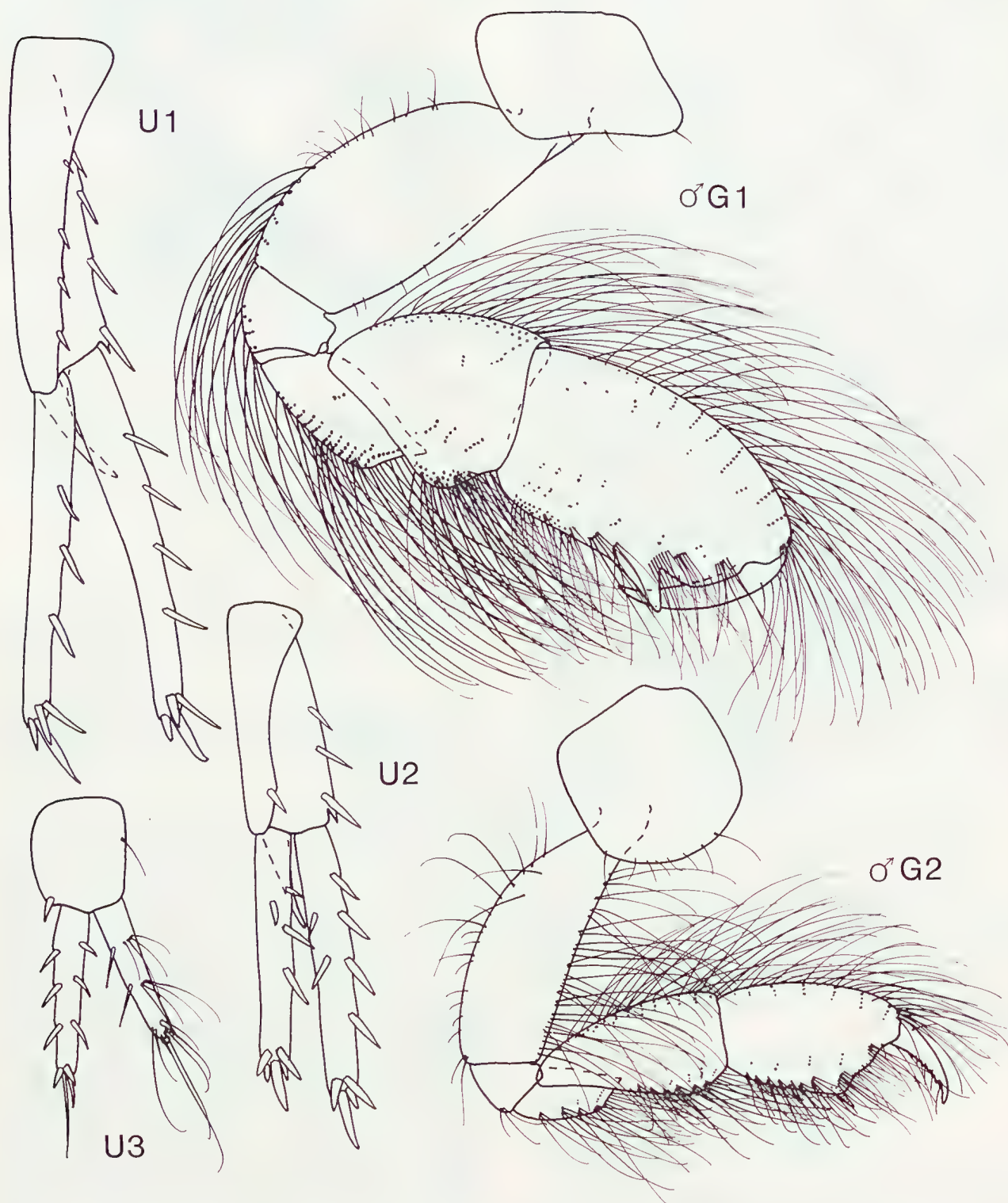


Fig. 52. *Protolembos arinyas* n.sp., male, Nooramunga.

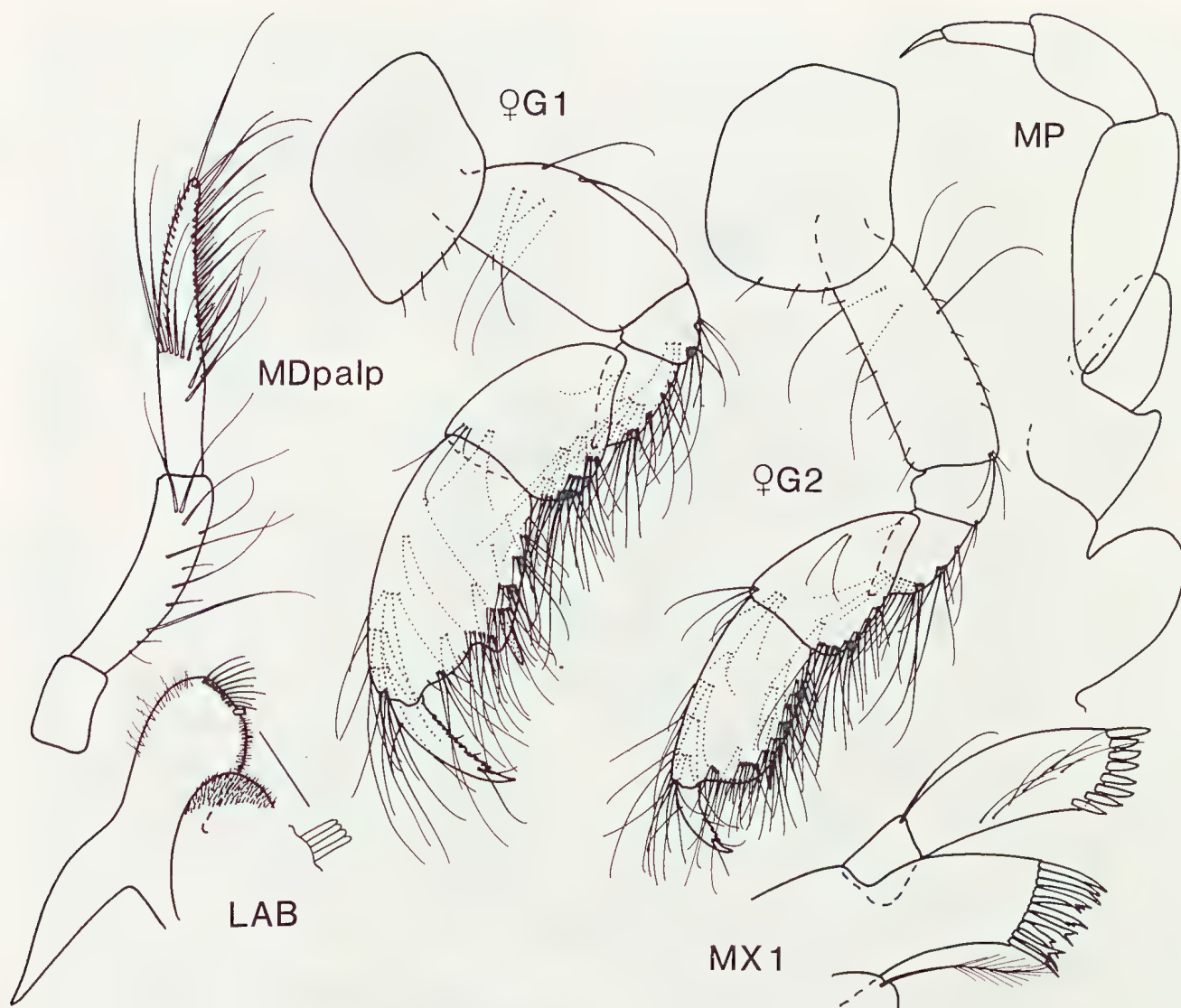


Fig.53. *Protosolembos arinyas* n.sp., male, female, Nooramunga.

Key to male *Globosolembos* of Australia

1. Gnathopod 1 palm defined by an acute tooth *G. ruffoi*
 —Gnathopod 1 palm excavate, lacking a tooth 2
2. Gnathopod 1 palm sharply angled at junction with excavation, uropods strongly spinous *G. lunatus*
 —Gnathopod 1 palm rounded at junction with excavation, uropods moderately spinous *G. excavatus*

Globosolembos ruffoi (Myers)

Fig. 54

Lembos ruffoi Myers, 1975b: 22, figs 68–75.
Lembos (Globosolembos) ruffoi Myers, 1985a: 341.
Lembos sp. Myers, 1985a: 365, fig. 235.
Globosolembos ruffoi Myers, 1988: 189.

Material examined. Queensland: 1 male, 2 females, patch reefs off Palfrey Island near Lizard Island, rubble with filamentous reds and encrusting reds, 7.7 m, 10 Jan 1982, B. Kensley, AM P37443; 1 male, reef off North Point, Lizard Island, rubble and clumps of *Amphiroa* from reef crest, 3 m, 12 Jan 1982, B. Kensley, AM P37444; 3 females, reef off North Point, Lizard Island, coral rubble at



Fig.54. *Globosolembos ruffoi* (Myers), male, Lizard Island.

base of cliff, some red algae, 18 m, 13 Jan 1982, B. Kensley, AM P37445; 2 males, between South Island and Palfrey Island, near Lizard Island, rubble with low algal turf from shallow ridge between islands, 2 m, 14 Jan 1982, B. Kensley, AM P37446; 2 males, 3 females, Lizard Island lagoon, rubble and low algal growth at base of patch reef, 10 m, 15 Jan 1982, AM P37447; 5 males, 5 females, 3 immature, + 3 slides, crest of patch reef in lagoon, rubble in algal turf from depression on crest, 2 m, 16 Jan 1982, B. Kensley, AM P37448; 4 males, 3 females, shelf between Palfrey and South Islands, coarse sand and sediment, 1 m, 19 Jan 1982, B. Kensley, AM P37449; 1 female, Sandbank Reef, north Queensland, 13°45'S 144°16'E, rubble washings from southwest end of reef, 8–10 m, 6 Dec 1982, I. Loch, AM P37450.

Habitat. Among coral rubble.

Distribution. East Africa, Queensland, ?India.

Globosolembos excavatus (Myers)

Lembos excavatus Myers, 1975b: 32, figs 76–82;—Ledoyer, 1982: 218, figs 104–105 (in part).

Lembos processifer.—Ledoyer, 1984: 35 (in part), fig. 16 ("forme 2"). (not *L. processifer* Pirlot, 1938: 330, figs 147–149).

Lembos (*Globosolembos*) *excavatus* Myers, 1985a: 363, fig. 234.

Globosolembos excavatus Myers, 1986: 285, figs 11–12.

Material examined. Queensland: 3 males, 5 females, 2 immature, fringing reef between Bird Islet and South Island, Lizard Island, coral rubble, 6.1 m, 7 Oct 1978, J.K. Lowry and P.C. Terrill, AM P29705; 5 males, 1 female, reef flat near research station, Heron Island, on *Holothuria atra*, low water, 4 Sept 1978, A. Waren, AM P28862.

Remarks. This species is figured by Myers (1986) and is not therefore figured here.

Habitat. Generally an amphipod associated with coral rubble. The record from *Holothuria atra* is unusual.

Distribution. East Africa, Madagascar, north-eastern Australia, New Caledonia, Tonga.

Globosolembos lunatus n.sp.

Figs 55–56

Type material. HOLOTYPE: male, 6.3 mm. Westernport, Vic., 38°29.78'S 145°06.28'E, 24 m, sand, 25 Nov 1974, NMV J14036. PARATYPES: 10 females, 9 males, 22 immature, same locality, NMV J13664.

Additional material. 1 male, Westernport, Vic., 38°28.70'S 145°06.07'E, 13 m, sand, 25 Nov 1974, NMV J13663.

Description. Body (in alcohol) without distinctive markings. Male pereon segments 2–4 with weak, rounded, sternal processes. Head anteroventral, corner strongly produced, acute. Labium outer plate distal margin with 5 spines. Mandible palp article ratio 2 : 5 : 6; article 3 elongate, falcate, posterior margin setae of variable length. Maxilla 1 palp article 2 with 8 distal spines. Antenna 1 peduncular articles

in the ratios 6 : 7 : 3; accessory flagellum with 5 articles, the terminal article rudimentary; primary flagellum broken in material examined. Antenna 2 peduncular articles 4 and 5 subequal, flagellum shorter than peduncular article 5, with 7 articles. Male gnathopod 1 coxa strongly expanded; carpus enlarged, subtriangular; propodus twice length of carpus, subovoid, palm straight, oblique, separated from posterior margin by shallow, evenly concave excavation delimited by a medial spine, propodus inner face with many rows of long setae; dactylus elongate strongly curved, opposable to medial spine. Female gnathopod 1 similar to that of male, but palm sinuous defined by weak tooth and spine and lacking posterodistal excavation. Male gnathopod 2 basis anterior margin straight or weakly concave, posterior margin moderately convex; carpus elongate, twice as long as broad; propodus shorter than carpus, anterior margin inflated; dactylus short, fitting evenly convex palm; anterior margin of carpus and propodus densely setose. Female gnathopod 2 coxa posteroproximal margin with row of stout setae; basis slender, anterior margin sinuous; carpus short subtriangular; propodus longer than carpus, parallel sided; dactylus short, fitting evenly convex palm; anterior margin of carpus and propodus less densely setose than that of male. Pereopods 3–4 dactylus short, less than one third length of propodus. Pereopods 5–6 missing. Pereopod 7 elongate, over half body length; basis with long setae on posterior margin only. Epimera 1–3 rounded. Uropod 1 peduncle with interramal tooth a little over one third length of peduncle; rami slender, strongly spinose; inner ramus the longer and a little longer than peduncle. Uropod 2 peduncle with inter-ramal tooth about half length of peduncle; rami elongate and strongly spinose; inner ramus distinctly the longer and longer than peduncle. Uropod 3 rami slender; inner ramus spinose; outer ramus setose, lacking a second article; both rami with long terminal setae.

Remarks. *Globosolembos lunatus* is closely related to *G. excavatus* and *G. indicus* but differs from both species in the strongly spinous uropods and in the sharply angled palmar termination of the hyperadult male gnathopod 1. The elongate male gnathopod 2 carpus is similar to that of *G. excavatus* but *G. lunatus* differs from that species in the larger carpus and weakly excavate posterodistal palmar margin of the male gnathopod 1, weakly developed sternal teeth of the male and strongly setiferous anterior margin (inner face) of the male gnathopod 1. The male gnathopod 1 of *G. lunatus* is quite similar to that of *G. indicus*, but that species has a crenulate palm to that appendage, a much less elongate carpus in the male gnathopod 2, long setae on the anterior margin of the basis of pereopod 7 and a more elongate carpus on the female gnathopod 2. Myers (1985a, 1986) pointed out the difficulties associated with the taxonomy of this genus which consists of numerous sibling species. It is principally a

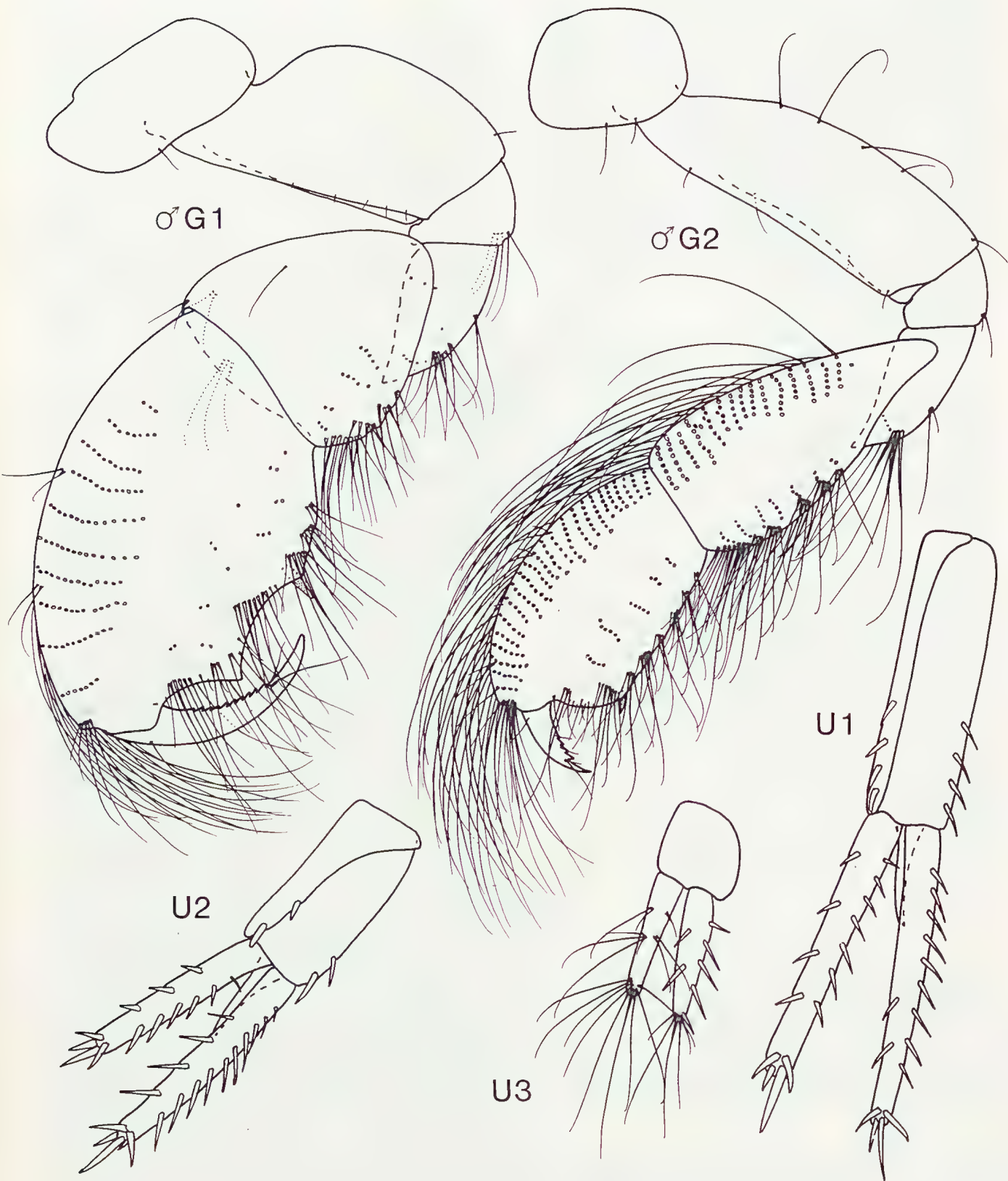


Fig.55. *Globosolembos lunatus* n.sp., male, Westernport.

circumtropical genus which reaches its greatest diversity in the Indo-Pacific. This is the first record of the genus from outside 30° N or S of the Equator.

Habitat. 13–24 m on sandy bottom.

Distribution. Victoria.

Etymology. From the latin *lunaris* = moon, referring to the shape of the excavation on the propodus of the male gnathopod 1.

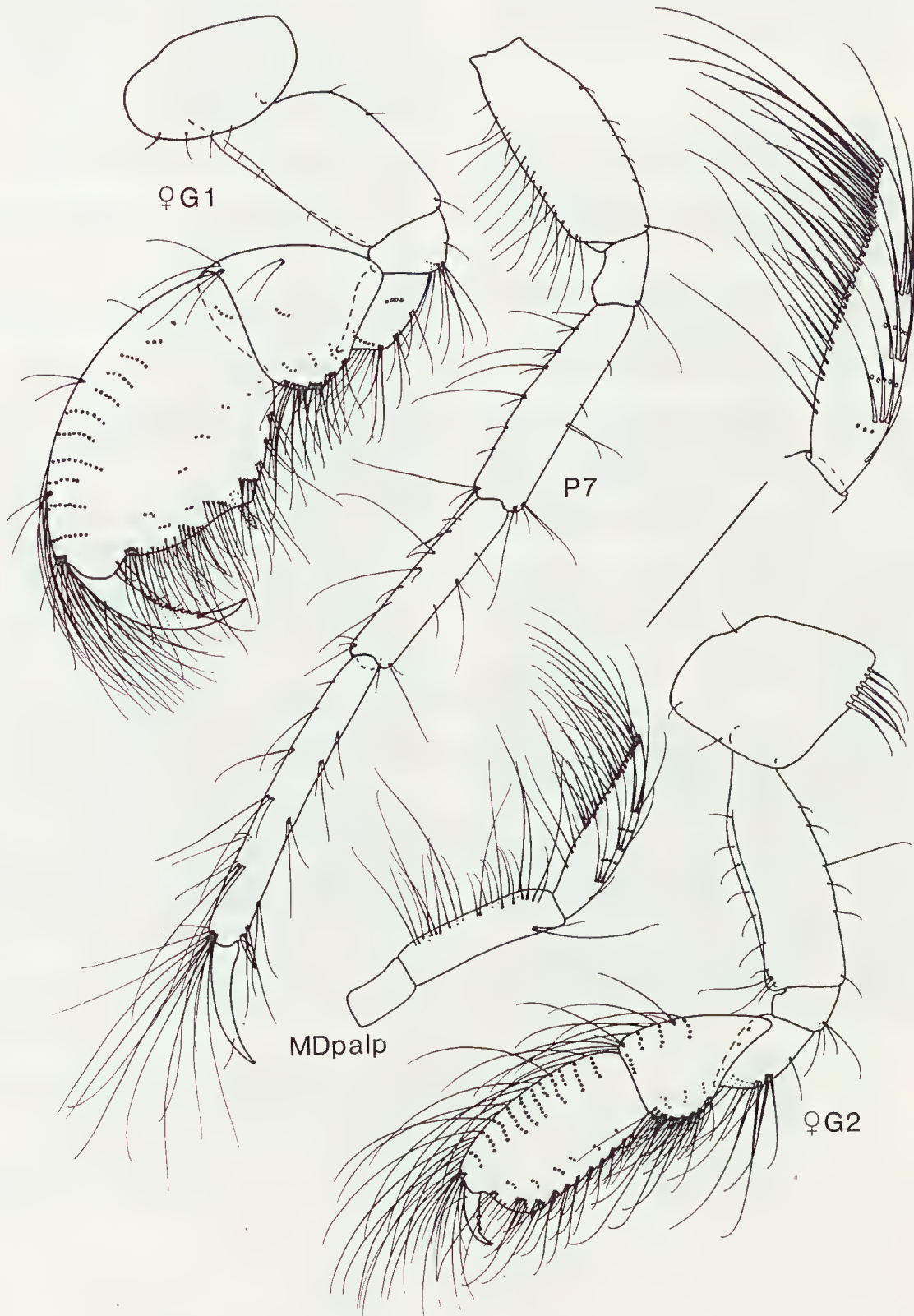


Fig.56. *Globosolembos lunatus* n.sp., male, female, Westernport.

ACKNOWLEDGEMENTS. I am indebted to the Australian Museum, Sydney for granting a Fellowship to enable me to carry out this work and for providing facilities and access to their extensive collections. I am grateful to Dr G.B. Poore for a loan of material from the National Museum of Victoria, and to Dr J.K. Lowry, Ms H. Stoddart, Ms P. Berents and Mr R. Springthorpe for their continuous help and encouragement.

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Pogonomys championi n.sp., a new murid (Rodentia) from montane western Papua New Guinea

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ABSTRACT. *Pogonomys championi* n.sp. is a medium-sized montane *Pogonomys* with grey-based ventral fur. It shares similarities with both *Pogonomys macrourus* and *Pogonomys sylvestris*, but also has some unique features. Thus far *P. championi* n.sp. is known only from the Telefomin and Tifalmin Valleys, Papua New Guinea, at altitudes of between 1,400 and 2,300 m. At these localities the species is common, and in the Telefomin area at the lower end of its altitudinal range, it is probably sympatric with *P. macrourus*.

Pogonomys championi n.sp. nests communally underground, with up to seven individuals sharing a nest. They ascend into trees at night to feed.

FLANNERY, T.F., 1988. *Pogonomys championi* n.sp., a new murid (Rodentia) from montane western Papua New Guinea. Records of the Australian Museum 40 (6): 333-341.

Dennis & Menzies (1979) clarified a long-standing confusion in murid taxonomy when they demonstrated, on the basis of morphometrics and chromosomes, that *Chiruromys* and *Pogonomys* are two distinct and not closely-related genera. In their concept of *Pogonomys* within New Guinea, three species were recognised: *P. macrourus* (Milne-Edwards, 1877), a medium-sized species from low-mid altitudes which has pure white ventral fur; *P. loriae* (Thomas, 1897), the largest species, also from low-mid altitudes and which almost always has pure white ventral fur; and *P. sylvestris* Thomas, 1920, the smallest, which is found at high altitudes and has grey-based ventral fur.

The aim of this study is to modify Dennis and Menzies' scheme by the recognition of a fourth species. This species is known only from mid-high altitudes in the western part of Papua New Guinea. When I first obtained specimens during 1984 I assumed they were *P. sylvestris*, but further study, and comparison with material held in the Australian Museum and the American Museum of Natural History, indicate that they represent an undescribed taxon.

Colours where capitalised follow Ridgway (1886). AM M = Australian Museum mammal specimen. AMNH = American Museum of Natural History

mammal specimen. MZB = Bogor Museum (Indonesia) mammal specimens. All measurements are in millimetres, and weights in grams. Dental nomenclature follows Musser (1981).

Systematics

Pogonomys Milne-Edwards, 1877

Pogonomys championi n.sp.

Figs 1, 2, 5, Tables 1, 2

Type material. HOLOTYPE AM M13502, male puppet skin and skull with dentaries. Collected by S. Van Dyck on 10 Feb 1984 at Ofektaman, Telefomin Valley, West Sepik Province, Papua New Guinea (5°04'S 141°34'E; P.N.G. Topographic survey sheet No. 7282 Telefomin, 1:100,000 series). Alt. 1,400 m. PARATYPES (n = 1) Sol River Valley, 2,300 m, (5°05'S 141°35'E), coll. T. Flannery, 14 Feb 1984: AM M13646, adult male skin and skull. (n = 13) Ofektaman, 1,400 m, (5°04'S 141°34'E), coll. S. Van Dyck, 9-12 Feb 1984: AM M13463-4, M13660, M13664, male skins and skulls; AM M13640, M13646, female skin and skulls; AM M13718-9, M13721-4, whole males in spirit; AM M13720, whole female in spirit. (n = 13) Tifalmin, 1,800 m, (5°07'S 141°25'E), coll. T. Flannery, L. Seri, 11 Apr 1987: AM M17727, M17729, M17731, males in spirit; AM M17728, M17730, M17732-3, females in spirit; AM M17721-2, M17725-6, male skins and skulls; AM M17723-4, female skins and skulls.

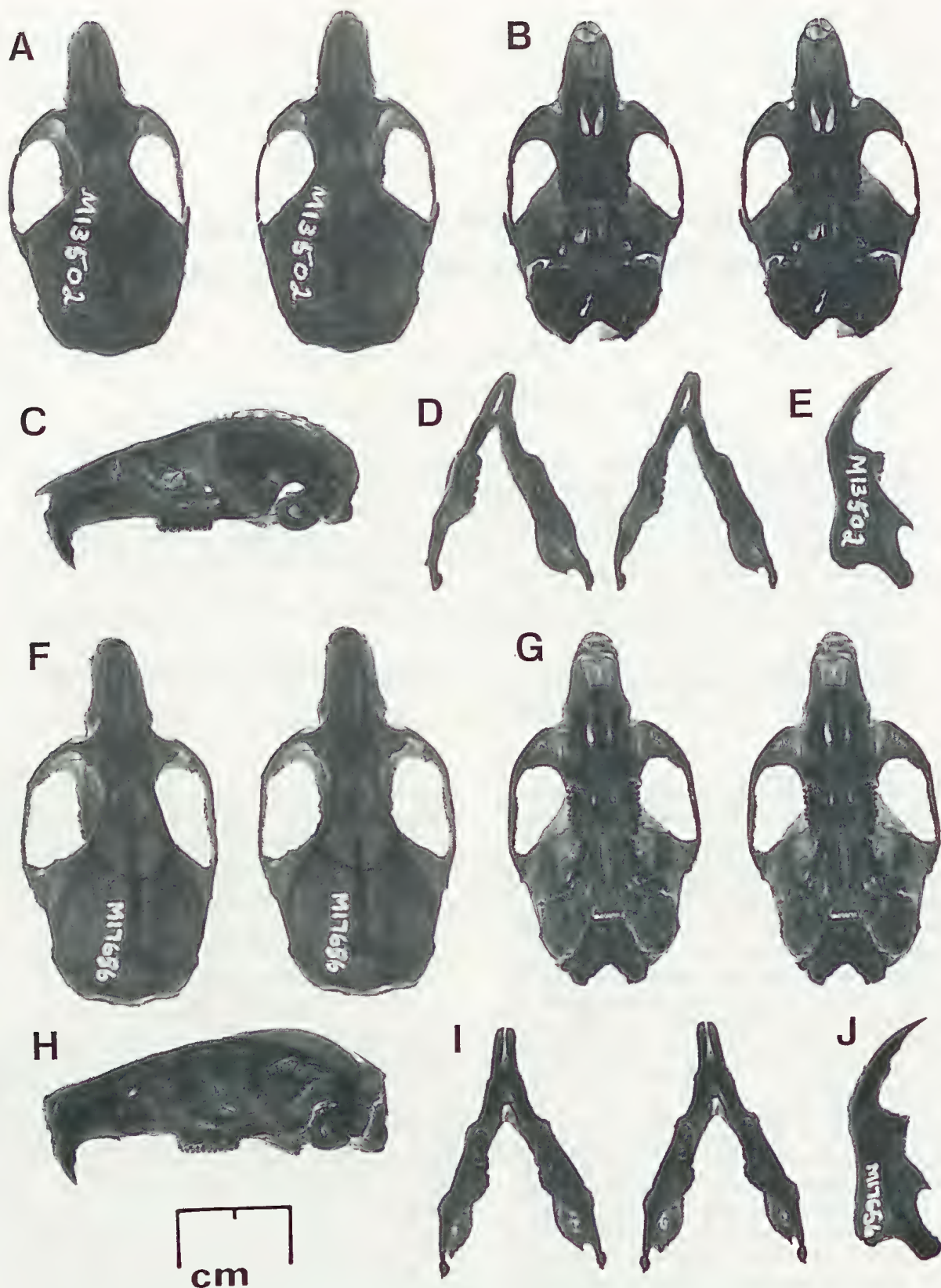


Fig.1. A, stereopair of dorsal C, lateral, and B, occlusal view of skull of the holotype of *P. championi* n.sp. (AM M13502: male); D, stereopair of occlusal view and E, buccal view of the dentary of AM M13502. F, stereopair of dorsal, H, lateral and G, stereopair of occlusal view of AM M17656, Male *P. macrourus*, Munbil, Star Mts, West Sepik Province. I, stereopair of occlusal view, and J, lateral view of dentary of AM M17656.



Fig.2. A, dorsal view and B, ventral view of puppet skin of the holotype of *P. championi* n.sp. (AM M13502), C, dorsal view and D, ventral view of puppet skin of AM M17656, *P. macrourus*, Munbil, Star Mts.

Diagnosis. *Pogonomys championi* n.sp. is unique within its genus in that the tail lightens, beginning from the distal end, with age. There is no clearly demarkated white tail tip, but rather the tail lightens imperceptibly distally. In aged individuals almost the entire tail can be ivory in colour.

Pogonomys championi n.sp. further differs from *P. lorae* in its much smaller size (see Tate, 1951), lack of white mottling on the tail, in always possessing grey-based ventral fur, in having a reddish tinge to the body sides, a drab brownish dorsal colouration,

and less well-developed superorbital crests. It further differs from *P. macrourus* in its lighter weight and shorter tail (Table 2), in possessing an ivory-coloured distal portion to the tail which gradually shades into the darker base, in having shorter, more rectangular tail scales (mean = 14.3 per cm opposed to mean = 12 for *P. macrourus*) which are generally arranged in more annular rings (Fig. 3), less well-developed supraorbital crests, grey-based ventral fur, and in being less rufescent dorsally and laterally. It further differs from *P. sylvestris* in having wider zygomata

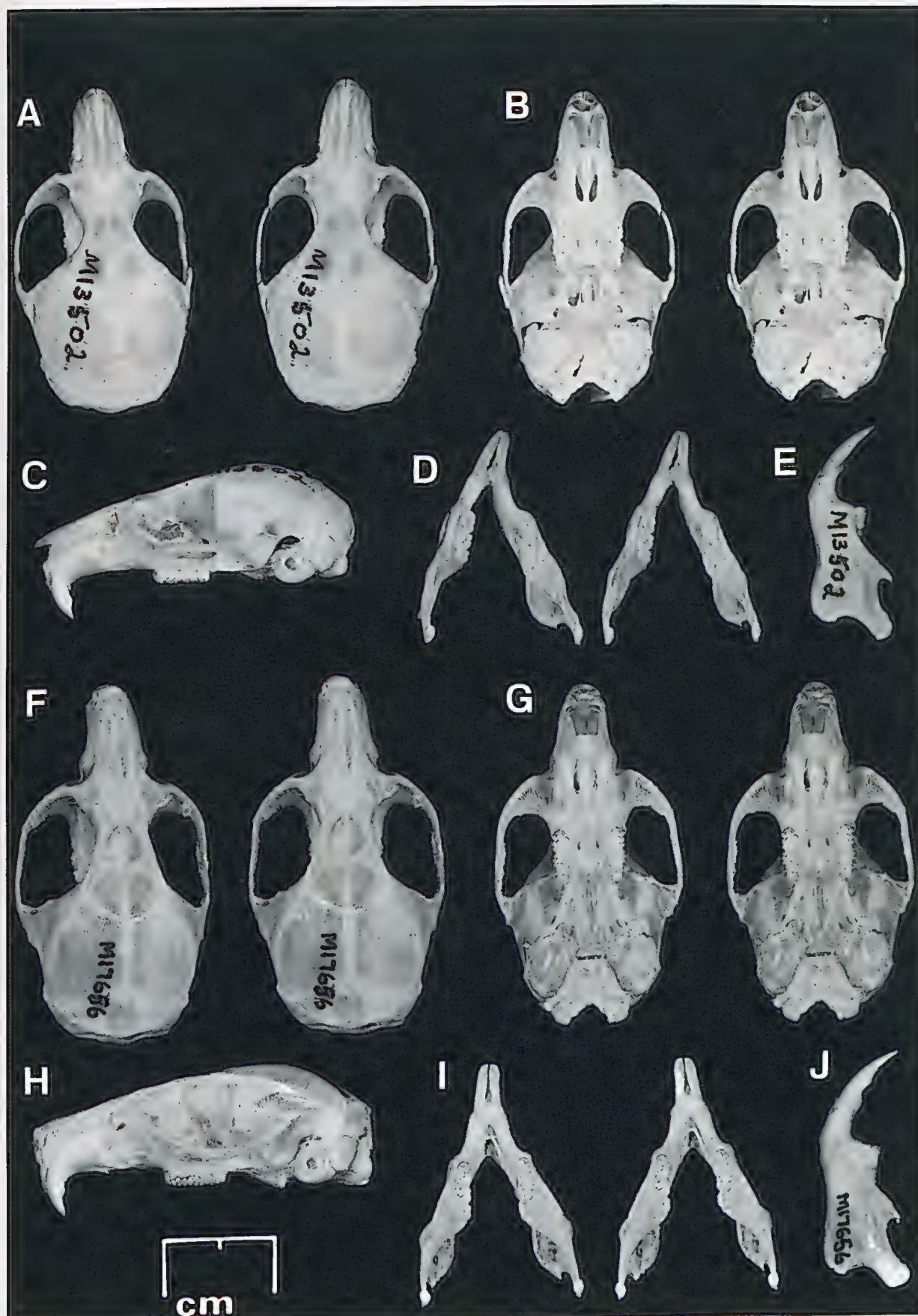


Fig.1. A, stereopair of dorsal C, lateral, and B, occlusal view of skull of the holotype of *P. championi* n.sp. (AM M13502: male); D, stereopair of occlusal view and E, buccal view of the dentary of AM M13502. F, stereopair of dorsal, H, lateral and G, stereopair of occlusal view of AM M17656, Male *P. macrourus*, Munbil, Star Mts, West Sepik Province. I, stereopair of occlusal view, and J, lateral view of dentary of AM M17656.

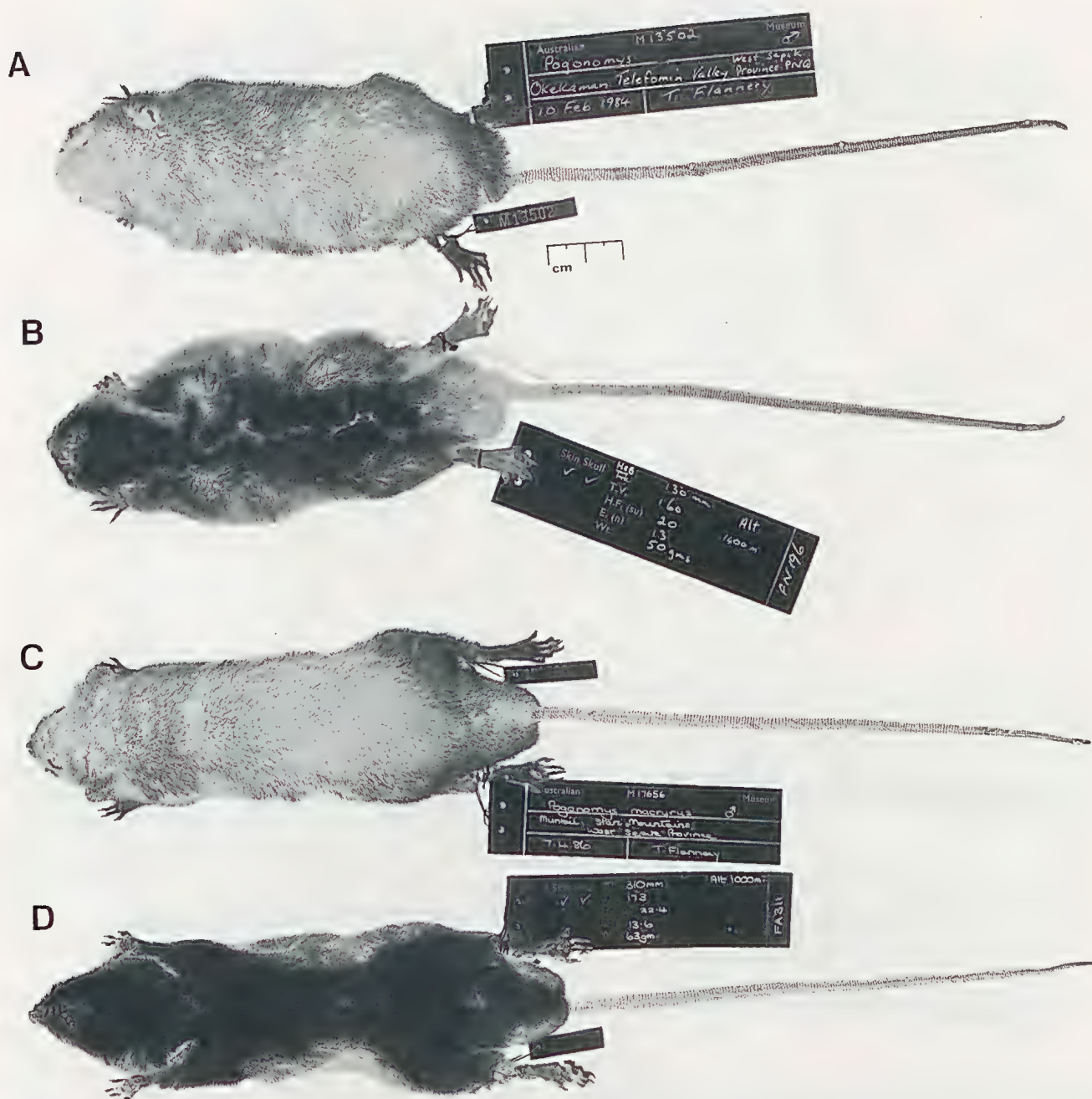


Fig.2. A, dorsal view and B, ventral view of puppet skin of the holotype of *P. championi* n.sp. (AM M13502), C, dorsal view and D, ventral view of puppet skin of AM M17656, *P. macrourus*, Munbil, Star Mts.

Diagnosis. *Pogonomys championi* n.sp. is unique within its genus in that the tail lightens, beginning from the distal end, with age. There is no clearly demarkated white tail tip, but rather the tail lightens imperceptibly distally. In aged individuals almost the entire tail can be ivory in colour.

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Table 1

Cranial and Dental Measurements (in mm) for *P. championi*. CBL = condylobasal length, BZW = Bizygomatic width, M¹⁻³L = length of upper molar row, M¹L = length of M1/, M1/W = width of M1/, IW = interorbital width, NL = nasal length, PL = palatal length, ZYG PW = zygomatic plate width, RH = rostrum height, X = mean, R = range, N = sample size, STD = standard deviation.

Total Sample				Holotype			Holotype		
CBL	X	30.0		29.5	BZW	X	17.4		17.3
	R	28.5-30.9		5		R	16.8-18.4		
	N	13				N	12		
	STD	0.87				STD	0.50		
M ¹⁻³ L	X	5.1		5.1	M ¹ L	X	2.3		2.3
	R	4.9-5.3				R	2.1-2.4		
	N	14				N	14		
	STD	0.12				STD	0.09		
M ¹ W	X	1.7		1.8	IW	X	4.5		4.6
	R	1.6-1.8				R	4.3-4.8		
	N	14				N	14		
	STD	0.06				STD	0.17		
Nasal L	X	10.5			PL	X	14.0		13.4
	R	10.0-11.4		10.7		R	13.4-14.8		
	N	14				N	14		
	STD	0.38				STD	0.49		
Zyg. Plate W	X	3.1		3.2	RH	X	5.8		5.8
	R	2.7-3.4				R	5.3-6.0		
	N	14				N	14		
	STD	0.19				STD	0.21		

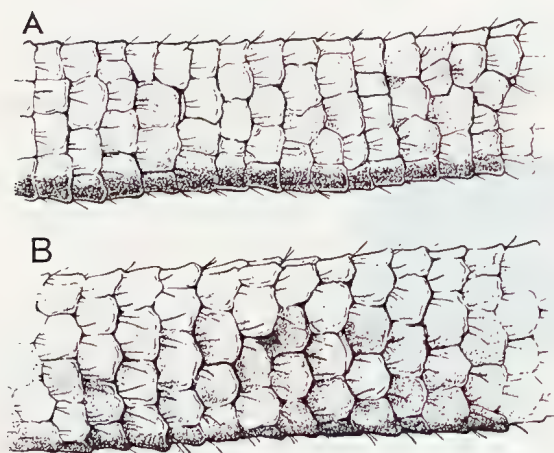


Fig.3. Tails of A, *Pogonomys championi* n.sp. (holotype, AM M13502) and B, *P. macrourus* (AM M17656, Star Mts) at 60 mm from tail base. X12.

(Table 1), tail scales which are arranged in a less annular pattern (Fig. 3), in lacking a distinct white tail tip (but rather having the pale distal portion of the tail intergrade into the darker base), in possessing more extensive white tipping on the ventral fur, and in being more rufescent on the body sides and dorsum.

Description. The following description is based upon the holotype. Variation within the paratype series is noted where it occurs.

Skull: incisive foramina short, bowed as in other *Pogonomys*, terminating 0.8 mm anterior to M1/. Two small palatal foramina present opposite M2/ on

palate. Rostrum narrow, but not as foreshortened as in species of *Chiruromys*. Palate terminates opposite T8-9 on M3/, no palatal thickening or postpalatal spine. Nasals do not overhang premaxillae, zygomatic plate of moderate breadth. Bullae are small. No supraorbital beading, only faint ridging on older specimens. Skull largely resembles that of *P. sylvestris*, but differs in broader zygomata (Table 1, Fig. 4). Dentary resembles that of other species of *Pogonomys*. No incisor tubercle.

Incisors: incisors do not differ in morphology from those of other species of *Pogonomys*. Enamel of lowers yellow, uppers deeper orange tinge.

Molars: molar cusps distinct, well defined as in all *Pogonomys* species. On M1/, T1-9 all present, usually form discrete conical entities. In some specimens (including holotype) T1 forms discrete cusp. On others is united with T2 by high enamel ridge. On holotype, accessory cusps are present between T1-2 and T2-3, cusps lacking or less well developed on other specimens. Distinct posterior cingulum extends posterobuccally from T8 also present on M1/.

M2/ shorter than M1/, consists of T1, T3-9. T3 greatly reduced or absent in some specimens. Distinct posterior cingulum present.

M3/ shorter and narrower than M2/. Consists of T1, 3, 4, 6, 8 and 9. T3 very small, present on all specimens examined. Tiny posterior cingulum projects directly posteriorly from between T8-9.

M1/ is a complex tooth. Prominent anterolingual and anterobuccal cuspid present, anterior to these are 2 small though distinct cusps. These are similar in morphology to the anterolingual and anterobuccal cusps, form miniature replicas of

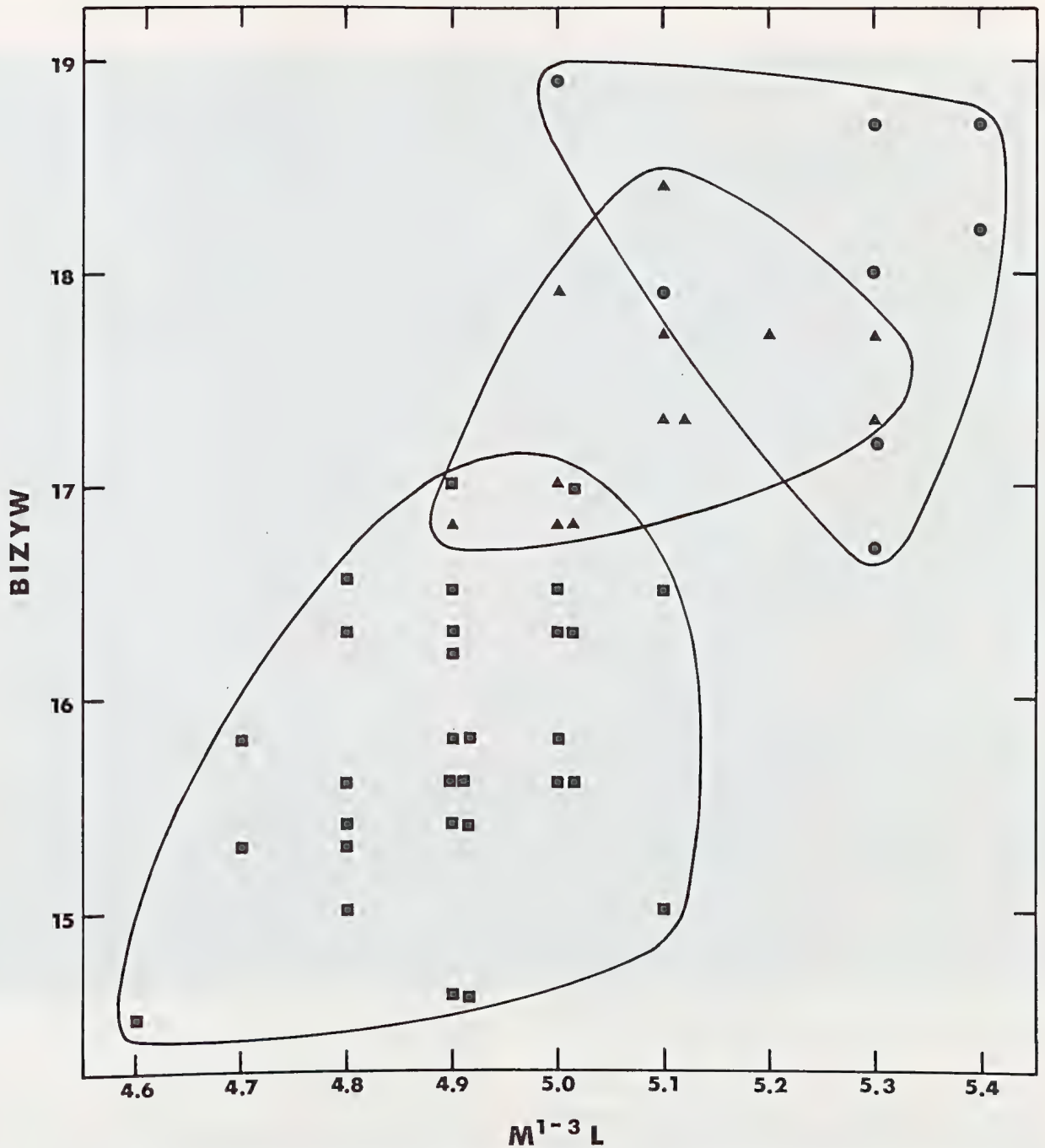


Fig.4. Plot (in mm) of bizygomatic width (vertical axis) against M1-3/ length (horizontal axis) for *P. championi* n.sp. (triangles), *P. macrourus* from the Telefomin area (circles) and *P. sylvestris* (PNG sample) (squares), adults only included.

them. Protoconid and metaconid subequal in size, similar in morphology to anterolingual and anterobuccal cuspids. Hypoconid and entoconid fused to form low transverse crest which narrows in median section, unlike more anteriorly-positioned cuspids. Low posterior cingulum oval-shaped, with long axis oriented transversely. Anteroposteriorly oriented anterobuccal crest positioned buccal to protoconid, subovate posterolabial cuspule positioned buccal to hypoconid. Overall, M/1 gives impression of being anteroposteriorly elongate structure which is ornamented by 5 transversely oriented sets of crests, each composed of 2 cusps with exception of posterior cingulum.

M/2 shorter than M/1. Consists of protoconid and metaconid which are united to form transverse crest, hypoconid and entoconid which are likewise joined. These 4 cusps subequal in size. Small, subovate posterior cingulum oriented as in M/1. Dumbbell-shaped anterolabial ridge present labial to protoconid, subovate posterolabial cusp buccal to hypoconid.

M/3 shorter and narrower than M/2. Consists of protoconid and metaconid which are united to form transversely-oriented crest as in M/2. Hypoconid and entoconid fused to form short, low crest. Subovate anterolabial cusp present buccal to protoconid.



Fig.5. Live male *Pogonomys championi* n.sp. from Tifalmin. (Photo H. Cogger).

Pelage: dorsal surface Sepia (Fig. 5). This overall appearance created by admixture of darker-tipped and more prominent guard hairs overlying Straw tipped underfur. Upon close inspection dorsal surface of pelage has "peppered" appearance. For basal four fifths of their length, hairs of dorsal surface are Blackish Slate. Sides of body have rufescent tinge, owing to more richly-tipped underfur, and thinning of guard hairs. Change to ventral colouration abrupt. Venter without guard hairs, underfur hairs being usually white tipped for distal third, with a Blackish Slate base. Underfur pure white on chin, in few specimens there is very small pure white patch on chest.

Distinct dark eye ring present, vibrissae black. Hands and feet sparsely covered dorsally with white hairs. Pads of feet and hands similar in position and size to those of other *Pogonomys*, unstriated. Mammary formula is $1 + 2 = 6$.

In middle of tail are 14.3 scales per cm ($R = 12-17$, $N = 11$, $STD = 1.35$) as opposed to 12.0 ($R = 10-13$, $N = 7$, $STD = 1.00$) for *P. macrourus* from the Telefomin area, and 12.2 ($R = 10-14$, $N = 19$, $STD = 1.12$) for *P. sylvestris* from the Bele River. Scales approximately 1 to 2 times as broad as long, roughly rectangular; arranged in distinct rings. 3 short hairs per tail scale (half to three quarters of scale length) that are barely visible with naked eye. Segment approximately 20 mm long on dorsal side of tail tip is prehensile. Juvenile specimens tail uniformly dark. Adult specimens tip lightens with age. No distinct white tip, rather tail lightens imperceptibly from tip to base. Old individuals most of tail Ivory in colour.

Etymology. I take great pleasure in naming this species in honour of Mr. Ivan Champion who has contributed so much to the development of Papua

Table 2

A. External measurements (in mm and gms) for *Pogonomys championi* (entire adult sample) and *Pogonomys macrourus* from the Telefomin area. All measurements taken on specimens in the field.

		<i>P. macrourus</i>		<i>P. championi</i>	
		♂	♀	♂	♀
head body length	X	126.2	122.2	123.7	120.5
	R	119-134	98-133	114-135	112-136
	N	5	12	20	8
	STD	5.85	9.50	7.24	9.96
tail vent length	X	174.7	163.5	157.6	158.3
	R	167-184	151-179.8	150-165	149-170
	N	5	12	19	8
	STD	7.26	7.81	4.06	6.73
hindfoot length	X	21.8	22.0	22.0	21.4
	R	19.0-22.8	20.8-24.3	20.0-24.0	20.5-23.0
	N	5	12	20	8
	STD	1.40	1.08	1.25	0.75
ear length	X	13.1	13.3	13.5	13.3
	R	12.4-13.5	12.4-14.5	12.0-16.0	11.0-14.0
	N	5	12	19	8
	STD	0.46	0.86	1.23	1.05
weight (grams)	X	59.4	58.8	49.4	51.5
	R	50-65	48-74	40-66	41.0-59.5
	N	5	12	16	11
	STD	5.94	7.73	8.09	6.02

B. External measurements for holotype of *P. championi*.

head body length	=	130
tail vent length	=	160
hindfoot length	=	20
ear length	=	13

New Guinea. Champion was the first European to cross New Guinea from the Fly to the Sepik, entering the Telefomin Valley in 1926. Thus it is fitting that one of the region's most attractive murids should bear his name.

Discussion

Systematics. *Pogonomys championi* n.sp. exhibits the diagnostic features of the genus *Pogonomys*. These are possession of a tail with non-overlapping scales which is upwardly prehensile; complex multi-cuspidate molars; and short, bowed incisive foramina.

Unfortunately, it has not been possible during the course of this study to examine the holotypes of *P. sylvestris* and *P. macrourus*, which are held in the British and Paris Museums respectively, because of lack of travel funds. The Mammal Section of the British Museum refuses to allow the loan of types, so the material could not be borrowed. However, the detailed descriptions and measurements of both types given in Tate (1951), along with the original descriptions, satisfy me that neither could be confused with *P. championi* n.sp. Furthermore, I have examined near topotypical material of *P. sylvestris*, which does not differ from the larger samples available to me from Papua New Guinea. Thus I am satisfied that current concepts of these taxa are correct.

Of the three currently recognised species of *Pogonomys* (*loriae*, *macrourus* and *sylvestris*), *P.*

championi n.sp. is most similar to *P. macrourus* and *P. sylvestris*. Indeed, the morphology of *P. championi* n.sp. is in many respects intermediate between the condition seen in these taxa. For example, *P. championi* n.sp. usually has some development of supraorbital ridges in older adults, while such features are absent in *P. sylvestris* but better developed in *P. macrourus*. The bi-zygomatic width is greater than is seen in *P. sylvestris* but smaller than in *P. macrourus* (Table 2, Fig. 4). The pelage and tail are likewise intermediate in some aspects of their morphology and colouration. For example, the dorsum of *P. championi* n.sp. is a richer red than in *P. sylvestris* but not as rufescent as in *P. macrourus*. The scales of the tail are arranged in rings, which are more distinct than in *P. macrourus*, but not as distinct as those of *P. sylvestris*. Unfortunately, the determination of polarity of many of these features within *Pogonomys* is not clear, so it is difficult to speculate regarding relationships.

Because of altitudinally correlated morphological variation in some New Guinean mammals (e.g. see Taylor *et al.* 1985) the possibility must be considered that *P. championi* n.sp. represents the end of an altitudinal cline involving it and *P. macrourus*. Many factors suggest that this is highly unlikely. A major one is that there is no clinal variation in the *P. macrourus* and *P. championi* n.sp. samples available to me from western Papua New Guinea. *Pogonomys macrourus* from 900 m are closely similar to those from 1,500 m, while *P. championi* n.sp. from 1,400 m

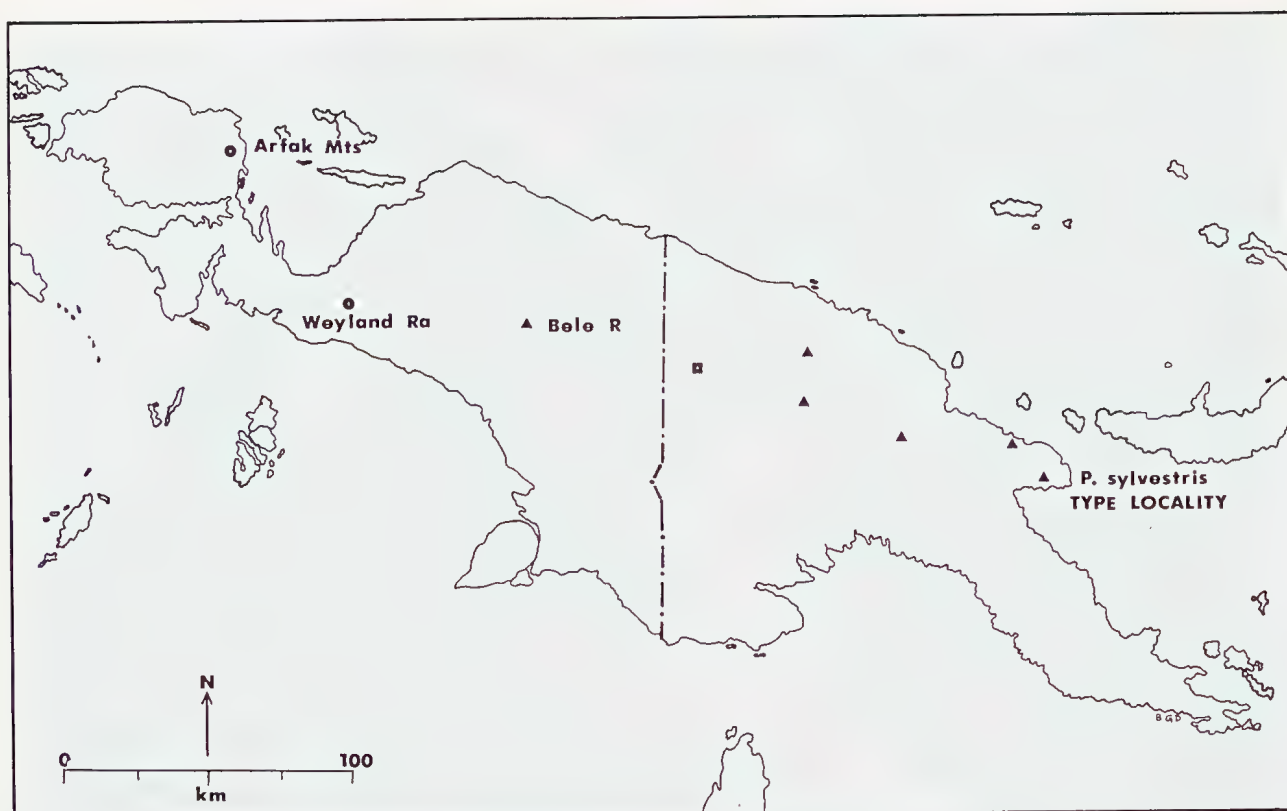


Fig.6. Distribution of *Pogonomys championi* n.sp. (square) and *P. sylvestris* samples (triangles) examined by me during this study, along with localities mentioned in the text.

are indistinguishable from the specimen from 2,300 m. Unless it is an extremely rapid step-wise one, these data make the existence of a cline seem unlikely. Furthermore, although the two species have not yet been found in sympatry, there is some indication that they overlap in altitudinal range. *Pogonomys macrourus* has been found at 1,350 m at Bogalmin village 3 km south of Telefomin Station, and *P. championi* n.sp. has been found at 1,400 m, 8 km northeast of the station (both in the Telefomin Valley). It would seem to be only a matter of time before they are found in sympatry. Furthermore, no intermediate or possible hybrid animals have been identified in the samples available to me.

Zoogeography. In an attempt to locate other samples of *Pogonomys championi* n.sp. I have examined records that may possibly relate to this species. Figure 6 shows the distribution of *P. championi* n.sp., samples of *P. sylvestris* used for this study, and the locations of other records of *Pogonomys* discussed here. As can be seen, records of *Pogonomys* with grey based ventral fur from western New Guinea are few. In the past, all have been referred to *P. sylvestris*. However, Rummler (1938) mentions some *P. macrourus* from the Weyland Range which have a fringe of grey based hairs around the margin of the venter. These animals probably are *P. macrourus*, but more information is needed before a firm assessment can be made. Records of *P. sylvestris* from western New Guinea

include those of Dollman (1930) from the Arfak Mountains, Rothschild & Dollman (1933) from the Weyland Range, and Tate (1951) from the Bele River and nearby Lake Habbema areas. Dollman's (1930) record has not been checked by recent reviewers. However, Tate (1936) reports upon the only two of the six animals available to him that were referred to *P. sylvestris* by Rothschild & Dollman (1933). One of these (No. 84) is a *Melomys*, while the other (No. 169) is a *Pogonomys* with pure white ventral fur, probably *P. macrourus*. These data suggest that Dollman was unclear as to the nature of *P. sylvestris*, and thus I consider both the Arfak and remaining Weyland Range records for this species as doubtful.

Nineteen specimens from the large series of *P. sylvestris* collected in the Bele River and Lake Habbema areas by the Third Archbold Expedition were loaned to me for examination. Sixty-four individuals were collected during the Expedition at 2,200 m, 18 km north of Lake Habbema, and a further two at 2,700–2,800 m, 9 km north of Lake Habbema. All material examined by me is from the first locality. Apart from their markedly larger size these specimens closely resemble *P. sylvestris* from Papua New Guinea, differing only in their slightly more drab dorsal colouration. They are probably separable at the subspecies level from *P. sylvestris* from Papua New Guinea. I am reasonably confident that *P. sylvestris* does not occur in southern West Sepik Province (the area from which *P. championi*

n.sp. is known), as a 4 year mammal survey, extending to altitudes of 3,200 m, and resulting in the collection of over 1,000 specimens, failed to reveal its presence there (Flannery & Seri in prep). This pattern of distribution for *P. sylvestris* and *P. championi* n.sp. is not readily explicable. More data is clearly needed regarding the distribution of these taxa before the nature of their geographic relationship becomes clear.

Biology. *Pogonomys championi* n.sp. and *P. macrourus* exist in close proximity in the Telefomin Valley. *Pogonomys championi* n.sp. occurs at 1,400 m at Ofektaman at the northern end of the valley, and at 2,300 m in the upper Sol River to the northeast of the valley. I have trapped *P. macrourus* at 1,500 m in the Nong River Valley just south of the Telefomin Valley, and at 1,350 m near Bogalmin Village in the middle of the valley. Although until now the two species have not been taken at the same station, I suggest that it is likely that they are partly sympatric based on the above distributional data. *Pogonomys macrourus* has been found between 900 and 1,500 m in the Telefomin area, while *P. championi* n.sp. occurs between 1,400 and 2,300 m. Thus if a zone of sympatry exists, it should occur at around 1,400–1,500 m.

Van Dyck (1986) describes the burrow of *P. championi* n.sp. under the name *P. sylvestris*. He reports that the burrows consist of an entrance hole 60 mm wide leading to an unbranching tunnel 2 m long. This tunnel terminates in a nesting chamber filled with dry vegetation (in one case dry bamboo). There is a short tunnel with an escape hatch immediately above the nesting chamber. It terminates in an exit hole 20–30 mm in diameter. One such burrow system contained five males and one female, while another contained only a female with two suckling young (in February). I have collected up to seven animals (4 adult males, 1 adult, 2 subadult females) from one burrow at Tifalmin. Specimens (e.g. AM 13646) have been captured feeding in low trees at night.

Summary

Pogonomys championi n.sp. is thus far known only from mid-high altitudes in western Papua New Guinea. It probably occurs sympatrically at approximately 1,500 m in the Telefomin area with *Pogonomys macrourus*. *Pogonomys championi* n.sp. nests communally in burrows, but ascends at night into trees to feed. Young have been collected in February.

ACKNOWLEDGEMENTS. I would like to particularly thank Dr Guy Musser of the American Museum of Natural History for his loan of specimens and valuable comments on a draft of this paper. Mr S. Van Dyck participated in the 1984 Telefomin Expedition and collected the fine series of *Pogonomys championi* n.sp. from Ofektaman, and for this I would like to extend special thanks. Thanks are also due to Tony and Maria Friend, for all the help that they gave

me during my time at Telefomin. Miss B. Duckworth prepared the figures for this work, and Mrs Tina Goh typed the manuscript. Finally, my wife Paula must be thanked for enduring my long absences while in the field.

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APPENDIX I

Material examined

Pogonomys sylvestris AM M19185 Duvi, Huon Peninsula, Madang Pro. AM M9624, 9570–80 Tomba, Hagen Ra, Western Highlands Pro. AM M8657, 8594–5, 8644–6, 8648–9, 8655, 8658, 8597–8, 8593, 8646, 8660, 7197, Kaironk Va, Schrader Ra. Madang Pro. AM M15428–9, 16239, 15442–51, Mt Erimbari, Chimbu Pro. AMNH150948–50, 151005–8, 151059–66, 151194–7, Bele R., Irian Jaya. MZB 8624–5 (by K. Aplin on my behalf), Bele R., Irian Jaya. All study skins and skulls.

Pogonomys macrourus AM M17248–53, 17257–67, 17635–6, 17677–8, 17681 Munbil, Star Mts West Sepik Pro. 17245 Bogalmin, Telefomin Va. West Sepik Pro. 17246–7 Yominbip, Thurnwald Ra. West Sepik Pro. 15867 Nong River Valley, West Sepik Pro.

Pogonomys loria AM M15412–3, 15415–26 Mt Erimbari, Chimbu Pro. M9576, 8 Korn, Upper Whagi Valley Western Highlands Pro. 15414, 15564, 15574, 6 Mt Sisa Southern Highlands Pro. 4135 Mt Lamington Northern Pro.

***Macroderma koppa*, a new Tertiary species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales**

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ABSTRACT. A new late Tertiary false vampire bat, *Macroderma koppa*, is described from the Big Sink doline of Wellington Caves, eastern central New South Wales. The new species appears to be the sister-group of the living Australian Ghost Bat, *Macroderma gigas*. Morphological features that distinguish the new species from *M. gigas* appear to be plesiomorphies shared with most other megadermatids.

HAND, S., L. DAWSON & M. AUGEE, 1988. *Macroderma koppa*, a new Tertiary species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales. Records of the Australian Museum 40(6): 343-351.

Until recently, all Australian fossil megadermatids had been identified as conspecific with (or very close to) the only living Australian megadermatid, the Ghost Bat *Macroderma gigas*. These fossils come from late Pleistocene and Holocene deposits in south-western Western Australia, the Flinders Range in southern central South Australia, north-eastern Queensland and north-eastern and eastern central New South Wales (see Molnar *et al.*, 1984; Fig. 1). Recently, the remains of Miocene species of the Australian endemic genus *Macroderma* have been recovered from limestone sediments on Riversleigh Station, north-western Queensland (Hand, 1984, 1985, 1987). In this paper a new late Tertiary species of *Macroderma* from New South Wales is described.

Fossil specimens described here were collected from breccia in the Big Sink, one of a complex of cave deposits occurring in Wellington Caves, New South Wales. These caves are formed in limestones of the Devonian Garra Formation which outcrops in low hills 1 km east of the Bell River approximately 7 km south of the town of Wellington (32° 35'S, 148° 59'E). They comprise at least five natural caves which have been expanded and greatly disturbed by fossil collection and phosphate mining over a period of 150 years. The history of fossil collection and mining from this locality has been described in detail by Dawson (1985). Cave nomenclature used here follows Dawson (1985, fig. 2).

Recent geological studies of the Wellington cave fills (Frank, 1971; Osborne, 1983) have indicated their considerable stratigraphic complexity. Osborne (1983) has hypothesised a depositional sequence for various stratigraphic units in the Wellington Caves system but the absolute ages of the units have not been determined. Osborne (1983), following Frank (1971), Francis (1973) and others, suggests that the oldest deposits within the caves could have been laid down in the Miocene. He cites faunal evidence suggesting that deposition of bone breccia occurred throughout the Pleistocene at least (Osborne, 1983).

Stratigraphically controlled excavations in the caves were made by the School of Zoology of the University of New South Wales in 1982-1987. Some preliminary results of this collection have been reported by Dawson (1985). Material described here was collected in October 1982 by M. Archer and students of the School of Zoology, University of New South Wales, from the Big Sink doline as part of a pilot study.

The species recovered from the Big Sink doline include: the macropodine *Protemnodon* sp. cf. *P. devisi* (the most abundant species); a plesiomorphic macropodine allied to *Wallabia* spp.; *Macroderma koppa* n.sp.; *Thylacinus* sp.; *Thylacoleo crassidentatus*; *Petauroides stirtoni* (a pseudocheirid otherwise known from the Hamilton local fauna of Victoria); several small dasyurids which are either



Fig.1. Map of Australia showing the distribution of *Macroderma* (solid triangles, extant populations of *M. gigas*; open triangles, fossil and subfossil remains). Open circles on map represent localities discussed in the text: 1, Cliefden Caves; 2, Wellington Caves; 3, Yessabah Caves; and, 4, Ashford Cave. (After Molnar *et al.*, 1984.)

new species or species otherwise poorly known from late Tertiary deposits (e.g. *Antechinus* sp. comparable to that described from the Floraville local fauna, Queensland by Archer 1982); a small bandicoot which probably represents a new Tertiary genus; a burramyid; and a new pseudomyine rodent. The non-mammalian fauna includes a species of *Tiliqua*, a scincid. The fauna is believed to be early to middle Pliocene in age (see Discussion) and is being described by L. Dawson (in prep.).

Institutional abbreviations used here are as follows: AM F — Australian Museum Fossil Collection; AM M — Australian Museum Mammal Collection (see Fig. 4); BMNH — British Museum (Natural History); UNSW WC — University of New South Wales, Zoology Museum, Wellington Caves Fossil Collection; WAM — Western Australian Museum (see Fig. 3).

CHIROPTERA Blumenbach, 1779

MICROCHIROPTERA Dobson, 1875

RHINOLOPHOIDEA Gray, 1825

MEGADERMATIDAE Allen, 1864

Macroderma Miller, 1907

Macroderma koppa n.sp.

Type material. HOLOTYPE (Fig. 2): the holotype (AM F69070) is a partial skull with associated dentaries. It

contains a complete dentition, i.e. $I_{1,2}$, C^1_1 , $P^4_{2,4}$, M^{1-3}_{1-3} . PARATYPES: a number of specimens have been selected as paratypes because each serves to illustrate features not represented in the holotype. The paratypes are: UNSW WC171, a skull fragment preserving the cheek, palate and part of the nasal regions; UNSW WC153, fragment with M^{1-3} and the maxillary base of the zygomatic arch; UNSW WC159 fragment preserving the back of the palate and P^4-M^3 ; UNSW WC158, fragment with P^4-M^3 ; UNSW WC170, maxillary fragment preserving the cheek region and P^4-M^2 ; UNSW WC173, 174 and 175, fragments of right C^1 s; UNSW WC176, fragment of left C^1 ; UNSW WC156, associated dentaries with I_1-M_3 ; UNSW WC173, dentary preserving P^4-M_3 , alveoli for C_1 and P_2 and base of ascending ramus; UNSW WC152 dentary fragment preserving M_{1-3} and base of ascending ramus; UNSW WC165, M_{1-3} ; UNSW WC177, a right C^1 ; UNSW WC178, a fragment of a left C_1 ; and UNSW WC179, a juvenile dentary without teeth. Other referred specimens are also lodged in the Zoology Museum at the University of New South Wales.

Diagnosis. The new species is referred to the megadermatid genus *Macroderma* which currently includes two species: the living Australian Ghost Bat *Macroderma gigas* and the extinct *M. godthelpi* of the Miocene of north-western Queensland (Hand, 1985). Species of *Macroderma* may be distinguished from other megadermatids (of the genera *Lavia*, *Cardioderma*, *Megaderma*, *Lyroderma* and the extinct monotypic *Necromantis*) by, among other features, their large size, enlarged heels of P^4-M^2 ,

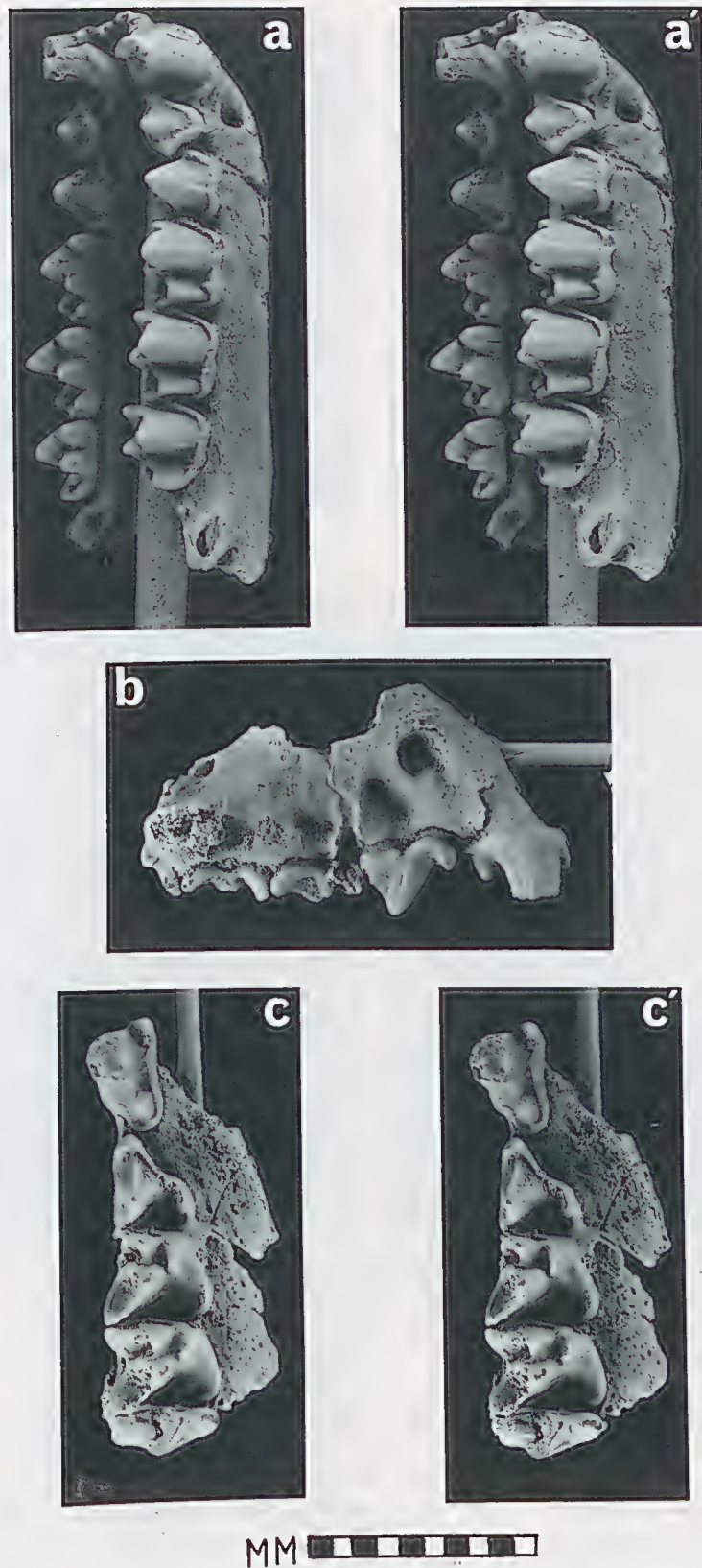


Fig.2. *Macroderma koppa* n.sp., AM F69070 (holotype), partial skull with associated dentaries and complete dentition. a-a', stereopairs, buccal-oblique view of mandibles with I₁, I₂, C₁, P₂, P₄, M₁, M₂, M₃; b, buccal view, right maxillary fragment; and, c-c', stereopairs, occlusal-oblique view, right maxillary fragment with C₁, P₄, M₁, M₂ and M₃. Photos by R. Oldfield.

more prominent paracone of C^1 and more robust buccal cingula of the lower molars (Hand, 1985).

The fossil species differs from the living *Macroderma gigas* in its retention of two infraorbital foramina, its poorly-developed nose-shield, its larger incisors and premolars, its less laterally compressed P_4 , its lower-crowned and more posteriorly recurved P^4 , and in its proportionately longer anterior tooth row.

Macroderma koppa differs from the Australian Miocene species *M. godthelpi* in its much larger size, relatively larger posterior infraorbital foramina, loss of P^2 , well-developed P^4 heel, its higher crowns and its more reduced pre-entocristids.

Type locality, lithology and age. The described material was collected from the southern wall of the Big Sink doline at Wellington Caves, NSW. Breccia from this position was identified by Osborne (personal communication, 1982) as part of the Big Sink Unit, the upper stratigraphic member of the Phosphate Mine Beds (Osborne, 1983). It consists of carbonate-cemented osseous sandstones interbedded with thin layers of structureless mud (Osborne, 1983). The unit is hypothesised to be older than (i.e. stratigraphically below) the breccia of the nearby bone-rich Bone Cave, identified by Osborne (1983) as belonging to the Mitchell Cave Beds. The Bone Cave fauna contains many species typical of Pleistocene deposits of eastern Australia (Dawson, 1985). Correlation of associated fauna with taxa otherwise known from better-dated deposits in Queensland and Victoria suggests that the Big Sink deposit from which the holotype was obtained is probably early Pliocene in age.

Description (based on the holotype and paratypes). Because the new species is clearly the closest sister-group of *Macroderma gigas* (see Discussion), it is described only in so far as it differs from *M. gigas*.

Maxillary fragments of *M. koppa* preserve cheek and orbital regions and part of nasal region; no sutures visible. In contrast to *M. gigas*, with single infraorbital foramen, 2 infraorbital foramina exhibited by this species (Fig. 3). Larger, anterior foramen opens onto face within fossa developed above anterior end of P^4 . Second, smaller foramen penetrates maxilla, possibly for lateral branch of trigeminal (facial) nerve, occurs within fossa developed above posterior end of P^4 . Larger fossa directed more anteriorly towards what would have been noseleaf; smaller fossa is directed anteroventrally towards lips or cheeks.

Nasal region of maxilla rises at approximately same angle as that of *M. gigas* (i.e. about 45° with respect to tooth row), is similarly gently concave. However, at least anterior part of nose-shield differs markedly from *M. gigas* in lack of bony lateral eminences (Fig. 4). Posterior (dorsal) region of nose-shield not preserved.

In their teeth, there is a great deal of morphological overlap between the two species. However, a combination of features in the anterior dentition distinguishes *M. koppa* from *M. gigas*. These features of *M. koppa* are described below.

C^1 , represented by 6 specimens, semicircular in basal outline with buccal side convex. Base of tooth posterobuccally swollen with marked notch separating base of paracone from base of large posterolingual accessory cusp. Latter cusp appears to be more discrete or isolated in *M. koppa* than *M. gigas*, being smaller in cross-sectional area and rising more steeply from base of crown. Posterolingually, tall but narrow cingulum commonly surrounds entire tooth but does not always enclose posterolingual accessory cusp. C^1 of *M. koppa* is comparable in size to C^1 of large specimens of *M. gigas* but lacks marked anteroposterior compressional flexure in base of lingual cingulum which characterises *M. gigas*.

P^4 is represented by 5 specimens which are comparable in width to, but much longer than, those of *M. gigas*. Difference in length appears due to elongation anterior to paracone so that principal cusp situated far more posteriorly along buccal edge of tooth than in *M. gigas*, accentuated by posteriorly recurved shape of paracone in *M. koppa*, shallow-angled rise of anterior crest of paracone from anterior cingulum and overall lower crown height of tooth. Anterior cingulum more pronounced in *M. koppa* with a cingular swelling occurring at its highest point. In lingual cingulum of broad heel, a distinct cingular cusp is developed which is also variably present within populations of *M. gigas*.

The morphology of M^1 , M^2 and M^3 appears to fall within the range of variation observed in *M. gigas*.

Lower incisors of *M. koppa*, known from holotype and UNSW WC156, far more robust than those of *M. gigas*, being at least one and one half times larger in crown area. Of what is known of incisors, their shape apparently similar to those of *M. gigas* with lateral incisors being much larger than inner incisors.

C_1 , represented by 6 specimens, similar in both size and shape to those of large individuals of *M. gigas*. Some intraspecific variation in *M. koppa*, however, appears to occur at lowest posterobuccal point of tooth (i.e. base of buccal edge of posteriorly flattened face of protoconid) where there is sometimes a break in otherwise high buccal cingulum.

P_2 , represented by 3 specimens, show considerable variation in depth and height of buccal cingulum. Tooth much wider and longer than in *M. gigas*, being markedly longer posterior to protoconid, so that in *M. koppa* protoconid occurs approximately midway along length of tooth.

P_4 , represented by 5 specimens, noticeably more robust than in *M. gigas* (Hand, 1985, fig. 12), being longer, wider, markedly less laterally compressed in area of protoconid. Longitudinal crest linking tip of protoconid to point on posterior cingulum appears to

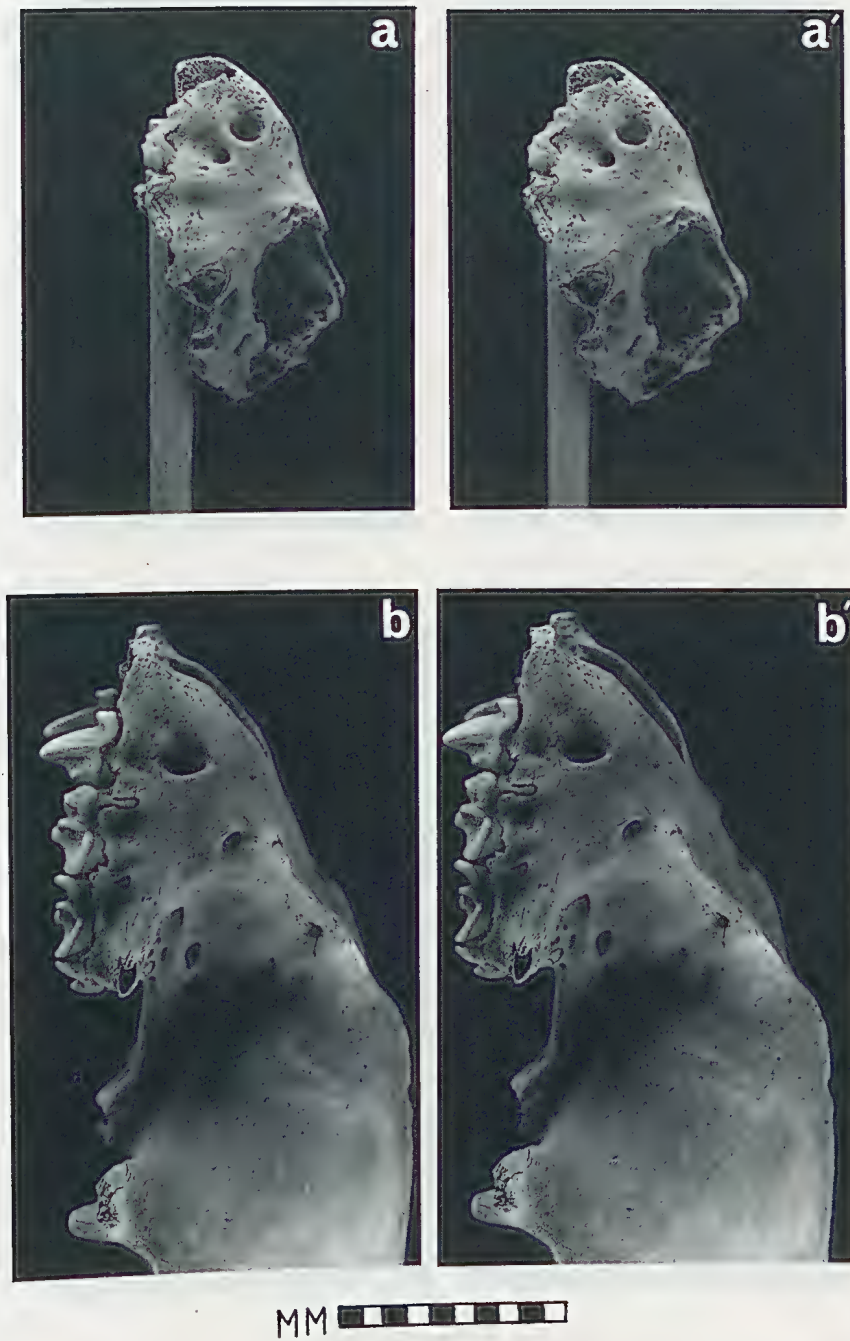


Fig.3. Comparison of the maxillas and number of infraorbital foramina in: a-a' (stereopairs), *Macroderma koppa* n.sp. (UNSW WC171); and b-b' (stereopairs), *Macroderma gigas* (WAM 65.12.191). Photos by R. Oldfield.

be more pronounced in *M. koppa*, often changes angle at base of protoconid. On either or both sides of crest (i.e. posterolingually and/or posterobuccally) depressions may be developed.

Morphology of M_1 , M_2 and M_3 (represented by minimum of 7 specimens each) appears to fall within range of variation in morphology observed in *M. gigas* (Hand, 1985, figs 13–15). In M_1 and M_2 ,

however, buccal cingulum swollen and ornate at point just anterior to protoconid. This feature, which occurs variably in populations of *M. gigas* (e.g. Hand, 1985, fig. 14), appears to be fixed in this population of *M. koppa* (but see below).

Table 1 gives measurements of the holotype, paratypes and referred specimens made to the nearest 0.1mm using a Wild MMS235 Digital Length-

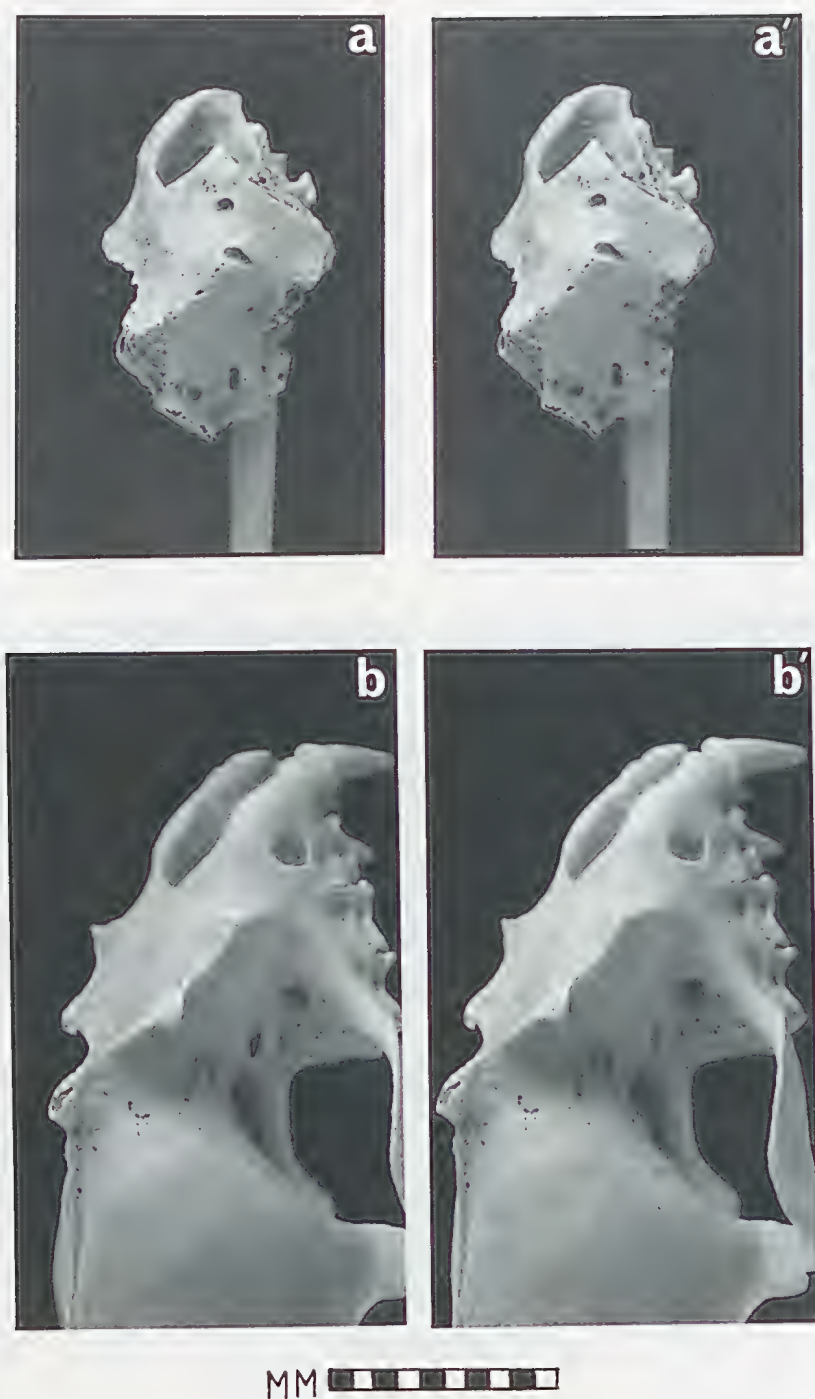


Fig.4. Comparison of the development of the bones comprising the frontal nose-shield in: a-a' (stereopairs), *Macroderma koppa* n.sp. (UNSW WC171); and, b-b' (stereopairs), *Macroderma gigas* AM M10190). Photos by R. Oldfield.

Measuring Set attached to a Wild M5A Stereomicroscope (see Hand, 1985, figs 9-10 for further explanation of measures).

Further comparisons. Other large specimens of *Macroderma* examined in this study include a dentary fragment from Australian Museum fossil collections (AM F47021; see Molnar *et al.*, 1984, fig. 3) collected from an unknown locality in the

Wellington Caves system. The specimen was probably collected last century or early this century and originally housed in the Mining Museum, Sydney before transfer to the Australian Museum (see Dawson, 1985).

Features of AM F47021 shared with *M. koppa* include its large size, lack of lateral compression of P_4 and its pronounced crest on P_4 running from the tip

of the protoconid to the posterior cingulum. For these reasons, the dentary fragment AM F47021 is tentatively referred to *M. koppa* n.sp. This specimen does not, however, exhibit a particularly swollen or ornate buccal cingulum on M_{1-2} .

Another specimen from "Wellington Caves", BMNH 42670b, discussed by Molnar *et al.* (1984) and housed in the British Museum, was not examined in this study.

Large Quaternary specimens of *Macroderma* from Yessabah Caves in north-eastern New South Wales and Cliefden Caves in eastern central New South Wales (see Fig. 1) are currently referred to *M. gigas* (Molnar *et al.*, 1984). Although larger than most specimens of *M. gigas*, because they are represented only by isolated dentaries lacking anterior teeth their identity remains in doubt.

The maxilla of a recently described partial skull recovered from Ashford Cave, north-eastern New

South Wales (see Fig. 1) (*Macroderma* sp. of Molnar *et al.*, 1984, figs 1,2) exhibits a single infraorbital foramen which excludes it from *M. koppa*. The lingual shape of the M^3 protocone, the feature singled out by Molnar *et al.* as being different, does not appear to differ significantly from larger samples of *M. gigas* and it is therefore referred to that species.

Etymology. The species is named after "Koppa", the mythological spirit believed by Australian Aborigines to have inhabited Wellington Caves (Lane & Richards, 1963). The reference to a spirit or ghost alludes to this species' close phylogenetic relationship with the living Ghost Bat, *Macroderma gigas*. Of the Big Sink fossil species so far identified, *M. koppa*, like its mythological counterpart, is probably the only one that actually inhabited the cave.

Table 1. Measurements of upper and lower teeth of the holotype (AM F69070), paratypes and referred specimens of *Macroderma koppa* n.sp. from Wellington Caves, New South Wales. In mm. (See Hand, 1985, figs 9–10 for further explanation of measures.)

Character	Holotype	Paratypes and referred specimens												
	AM	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	UNSW	AM
	F69070	WC152	WC162	WC161	WC163	WC154	WC158	WC153	WC164	WC156	WC159	WC170	F47021	
Length C ¹ –M ³	16.7													
Length P ⁴ –M ³	13.1										12.8			
Length M ¹ –M ³	9.4													
P ⁴ buccal length	4.1						4.2				3.7	4.0		
M ¹ buccal length	4.1						4.1	4.0			4.2			
M ² buccal length	3.8				3.6		3.8	3.9				4.2		
M ³ buccal length	2.0							1.9						
P ⁴ lingual length	4.1											4.2		
M ¹ lingual length	4.0													
M ² lingual length	3.6				3.9							3.6		
P ⁴ width	3.5											3.2		
M ¹ width	4.4						4.3	4.1						
M ² width	4.5				4.4		4.5	4.6				4.1		
M ³ width	4.3						4.5							
Dentary depth below														
M ₂ protoconid	4.2	4.5								4.4				
Length C ₁ –M ₃	19.7													
Length P ₄ –M ₃	15.0													
Length M ₁ –M ₃	12.1													
P ₄ length	3.4	3.2								3.1			3.6	
P ₄ anterior cingulum														
to protoconid														
length	1.4									1.4			1.9	
M ₁ length (in situ)	4.2	3.7								3.9			3.8	
M ₂ length (in situ)	4.2	4.1								4.0			3.9	
M ₃ length (in situ)	4.0													
M ₁ trigonid length	2.7	2.3	2.5	2.2						2.6			2.5	
M ₁ talonid length	1.5	1.5	1.4	1.6						1.4			1.4	
M ₂ trigonid length	2.5	2.4		2.3					2.3	2.5			2.4	
M ₂ talonid length	1.6	1.6		1.3					1.6	1.5			1.5	
M ₃ trigonid length	2.5					2.5			2.2	2.5				
M ₃ talonid length	1.4					1.4			1.7					
P ₄ width	2.3		2.0							2.1			2.1	
M ₁ trigonid width	2.4	2.3	2.3	2.1						2.4			2.2	
M ₁ talonid width	2.5	2.4	2.3	2.2						2.5			2.4	
M ₂ trigonid width	2.8	2.4		2.4					2.4	2.6			2.5	
M ₂ talonid width	2.6	2.3		2.2					2.3	2.5			2.5	
M ₃ trigonid width	2.5					2.2			2.4				2.6	
M ₃ talonid width	2.1					1.6			1.9					

Discussion

Recent geological studies by Frank (1971, 1972, 1975), Francis (1973) and Osborne (1983) have shown that bone-bearing stratigraphic units in Wellington Caves are not contemporaneous. Osborne (1983) suggests that they represent a minimum of three periods of deposition ranging from at least the Pliocene to late Pleistocene. The Big Sink Unit has been identified as being the upper member of the Phosphate Mine Beds (Osborne, 1983) and, on the basis of faunal evidence, is hypothesised to have been deposited during the early to middle Pliocene.

This faunal evidence is provided by a number of studies in progress involving stage-of-evolution comparisons with mammalian taxa from the stratigraphically higher (i.e. younger) Bone Cave sediments, as well as other better-dated Australian Pliocene and Pleistocene fossil mammal assemblages. For example, the dominant macropodine of the Big Sink local fauna, *Protemnodon* sp. cf. *P. devisi*, differs only slightly

(Dawson, 1985) from *P. devisi* which is known only from the early Pliocene-aged Chinchilla Sand fauna of south-eastern Queensland (Bartholomai, 1973). A Pliocene age is also supported by the presence of *Thylacoleo crassidentatus* and, among the small marsupials, *Petauroides stirtoni* and a unique peramelid which are otherwise known only from the early Pliocene Hamilton local fauna of Victoria. A Pliocene age is also indicated by the conspicuous absence of many species which are typically found in Pleistocene deposits (e.g. species of *Macropus*, *Procoptodon*, *Diprotodon optatum*, *Sthenurus atlas*, several rodent and dasyurid species, etc.) and which are abundantly present in the Bone Cave deposits of Wellington Caves (Dawson, 1985).

The Big Sink's *Macroderma koppa* is clearly distinguished from all known modern and Pleistocene specimens of *M. gigas* by the retention of two infraorbital foramina on the facial side of the maxilla. The double foramen state is a plesiomorphic (or primitive) condition present in most megadermatids (Hand, 1985) with the exception of

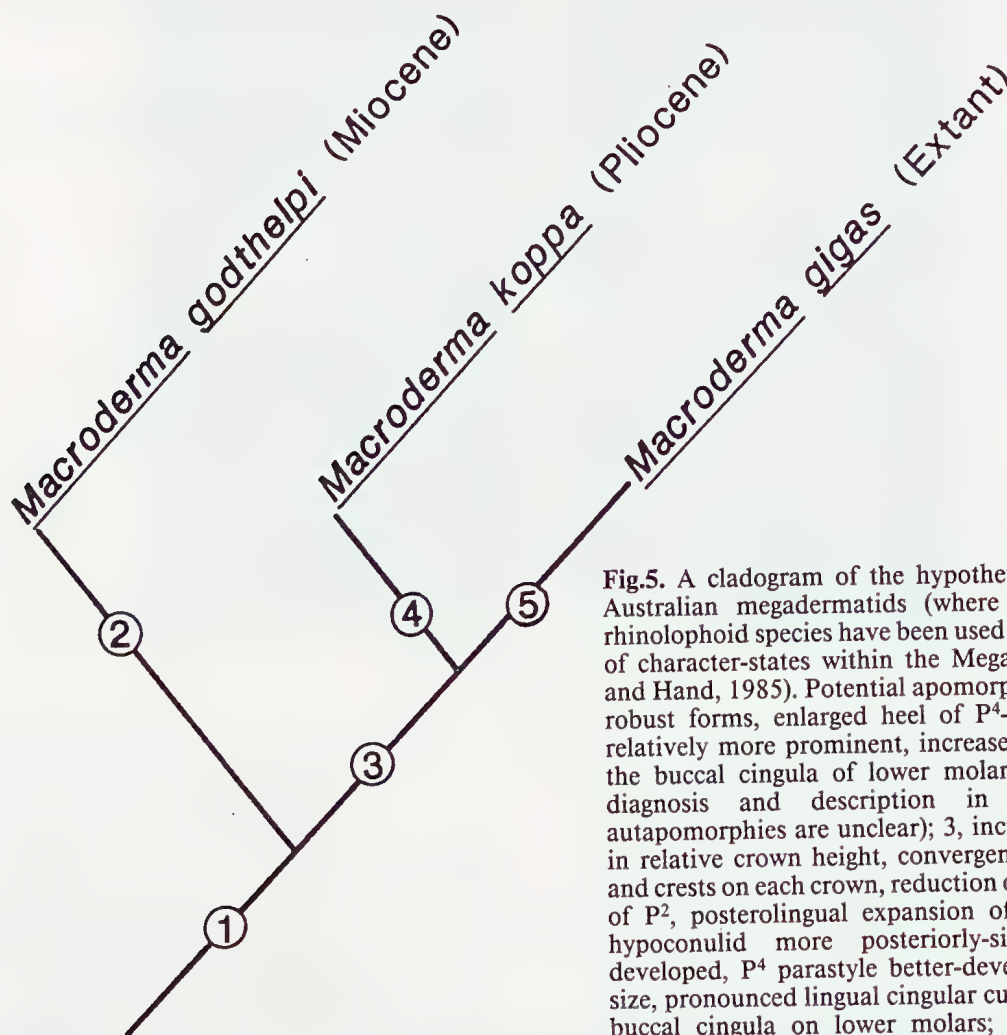


Fig.5. A cladogram of the hypothetical relationships of Australian megadermatids (where nycterid and other rhinolophoid species have been used to determine polarity of character-states within the Megadermatidae; see text and Hand, 1985). Potential apomorphies are as follows: 1, robust forms, enlarged heel of P^4 - M^2 , paracone of C^1 relatively more prominent, increase in the robusticity of the buccal cingula of lower molars; 2, (see systematic diagnosis and description in Hand, 1985; but autapomorphies are unclear); 3, increase in size, increase in relative crown height, convergence of principle cusps and crests on each crown, reduction of preentocristids, loss of P^2 , posterolingual expansion of the heel of P^4 , M^2 hypoconulid more posteriorly-situated and better-developed, P^4 parastyle better-developed; 4, increase in size, pronounced lingual cingular cusp on P^4 , more robust buccal cingula on lower molars; 5, single infraorbital foramen, relative shortening of the anterior tooth row, elaboration of frontal nose-shield, lateral compression of P^4 , higher crowned and less posteriorly recurved P^4 .

species of the French early Tertiary genus *Necromantis* (Revilliod, 1922) and all specimens of *M. gigas*. *Necromantis adichaster* and *M. gigas* exhibit a single infraorbital foramen. Because *N. adichaster* lacks most of the derived features that *M. gigas* shares with other living and fossil megadermatids (e.g. loss of P_3 , a posteriorly extended palate, well-developed heels on P^4 - M^2 and an expanded paroccipital shelf) and exhibits a number of striking autapomorphies (e.g. a conspicuously flattened skull, shortened face and inclined rectilinear sagittal crest), the shared state of the single foramen in *N. adichaster* and *M. gigas* is interpreted to be the result of evolutionary convergence (Hand, 1985).

Macroderma koppa and *M. gigas* appear to be very closely related. *Macroderma gigas* appears to be a relatively recent offshoot from an ancestral population of the kind represented by *M. koppa*. A phylogenetic hypothesis involving these species and the Australian Miocene *M. godthelpi* is given in Fig. 5. Determination of the polarity of character-states in this phylogenetic analysis has been facilitated by common recognition (following Miller, 1907) of a Megadermatidae-Nycteridae sister-group relationship within the Rhinolophoidea (see Hand, 1985).

Features that distinguish *M. koppa* from *M. gigas* include its relatively poorly-developed nose-shield, more robust incisors and premolars, less laterally compressed P_4 , lower crowned but larger P^4 and its proportionately longer anterior tooth row. In these plesiomorphic features, *M. koppa* more closely resembles the Australian Miocene species *Macroderma godthelpi* than the living *M. gigas* (Fig. 5).

Macroderma koppa is the second fossil megadermatid to be described from Australia. Four new but as yet undescribed Miocene megadermatids and a tiny Pliocene species have been recently recovered from deposits on Riversleigh Station (Hand, 1987). This diversity indicates that *M. godthelpi*, *M. koppa* and *M. gigas* are representatives of what was once an extensive Australian radiation of false vampires, second only, perhaps, to that of the European Tertiary.

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Brachycalanus rothlisbergi, a new species of planktobenthic copepod (Calanoida, Phaennidae) from the Gulf of Carpentaria, Australia

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ABSTRACT. *Brachycalanus rothlisbergi* n.sp. females sampled from the Gulf of Carpentaria are described and figured. Comparisons are made between this species and the four others belonging to this genus.

OTHMAN, B.H.R. & J.G. GREENWOOD, 1988. *Brachycalanus rothlisbergi*, a new species of planktobenthic copepod (Calanoida, Phaennidae) from the Gulf of Carpentaria, Australia. Records of the Australian Museum 40 (6): 353-358.

During studies of copepods of the Gulf of Carpentaria, females of a new species of copepod from the family Phaennidae were encountered, and are described below. This species was taken in stepped-oblique hauls from near-bottom to the sea surface using plankton nets of mesh aperture size 140 μ m. The specimens were examined, measured and dissected in glycerine/water medium and drawings were all made using a Leitz HM-LUX microscope with the aid of a camera lucida.

Brachycalanus rothlisbergi n.sp.

Figs 1,2

Type material. Type materials are deposited in the Queensland Museum (QM) as follows: female holotype of total length (TL) 1.57 mm, 1 female paratype. Reference nos. QM W12198, QM W12199.

Type locality. Gulf of Carpentaria, 11°55.5'S, 138°49.5'E.

Material examined. 1 female, sample no. 28A2, 14°01.5'S, 138°E, 19 Aug 1975; 1 female, sample no. 447A4, 11°55.5'S, 138°49.5'E, 7 Nov 1977; 2 females, sample no. 971A3, 14°S, 140°E, 11 May 1977 (see Rothlisberg & Jackson (1982) for sample details).

In the following descriptions medial refers to that border of an appendage or segment which faces the

midline of the body and lateral to that border directed toward the lateral surface of the body.

Description of female (Figs 1A-F, 2A-H). *Size:* TL (tip of prosome to end of furcal rami) is 1.61 mm (mean from 3 measurements range 1.57-1.68 mm standard deviation 0.0214). Prosome length-to-width ratio 1.91:1, prosome to urosome length ratio 4.36:1.

Body very robust, oval in dorsal view, with relatively short urosome (Fig. 1A). In lateral view, head smoothly rounded, ending in short rostrum with 2 filaments. Head separated from first thoracic somite, fourth and fifth thoracic somites fused. Very distinct setae arise near midlateral surface of third thoracic somite (Fig. 1A,B). Posterior thoracic margins symmetrical, margins appear triangular in shape but are well rounded posteriorly both in dorsal and lateral views.

Urosome 4-segmented, surfaces of each somite covered densely with spinules. Anal segment extremely short, relative lengths of visible somites as follows:

Somites	1	2	3	4	caudal rami	
Proportions	47	20	13	11	9	= 100

Caudal rami symmetrical, with 4 subequal apical

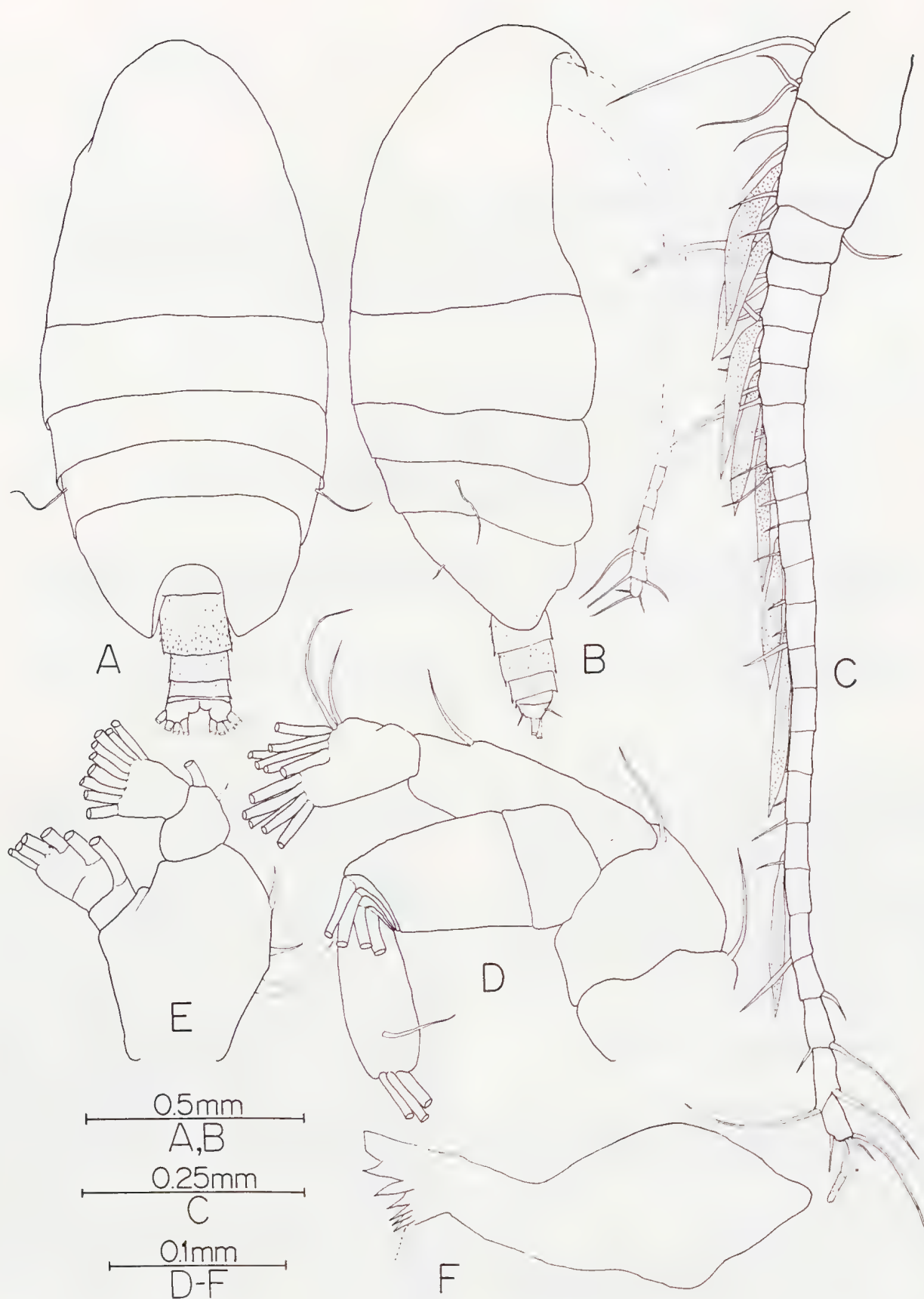


Fig.1. *Brachycalanus rothlisbergi* n.sp. female; A – dorsal view; B – lateral view; C – 1st antenna; D – 2nd antenna; E – mandibular palp; F – mandibular blade.

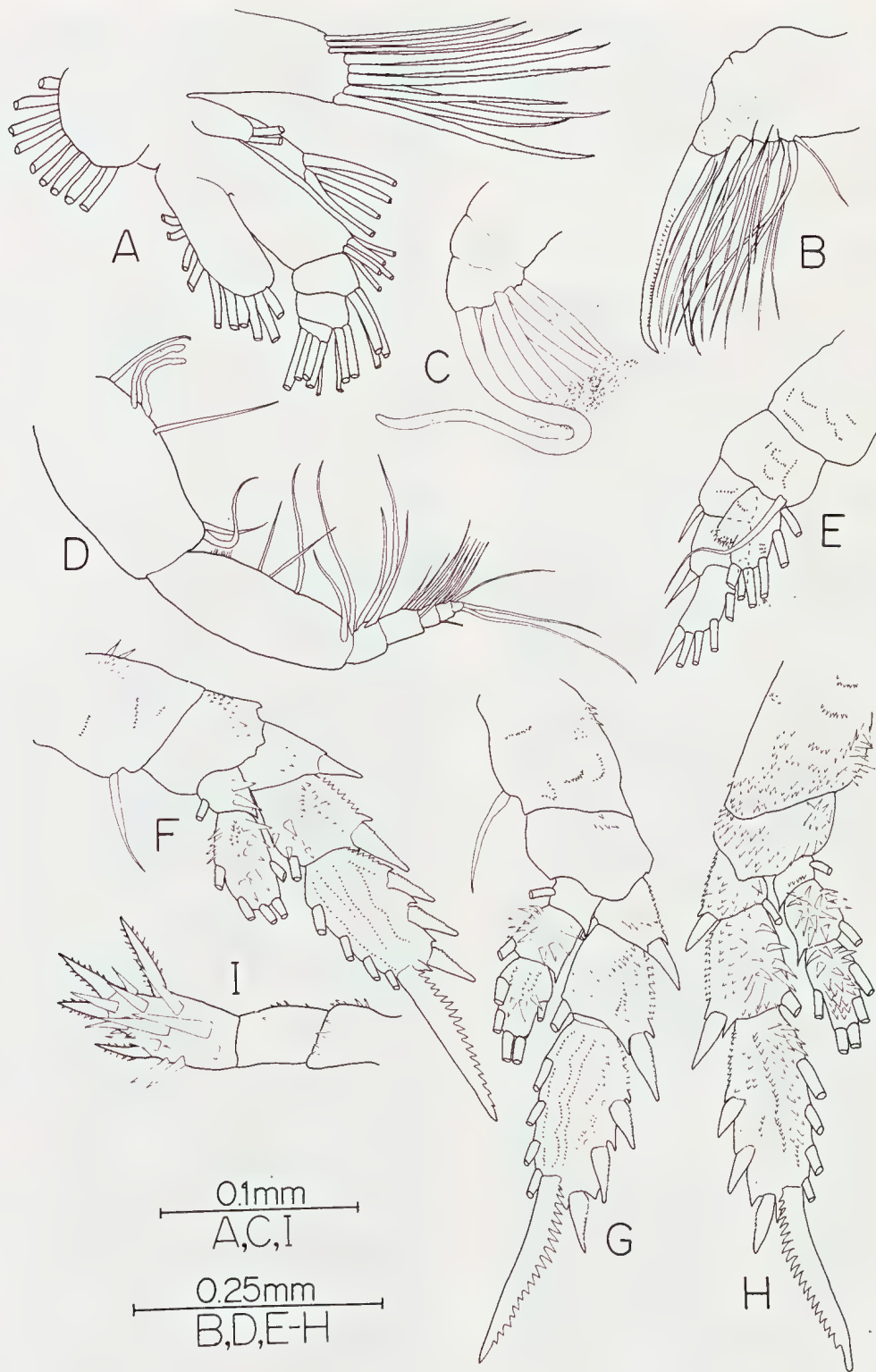


Fig.2. *Brachycalanus rothlisbergi* n.sp. female; A – 1st maxilla; B – 2nd maxilla; C – endopod of 2nd maxilla; D – maxilliped; E – 1st leg; F – 2nd leg; G – 3rd leg; H – 4th leg; I – 5th leg.

setae (Fig. 1A) and 2 minute setae (Fig. 1B). Length to breadth ratio of caudal ramus is 0.75:1.

First antenna 24-segmented, reaches to middle of last thoracic somite. The segments are of various sizes, the proportional lengths are given below:

Segments	1	2	3	4	5	6	7	8	9	10	11	12	13
Proportions	91	75	42	23	37	33	33	55	29	23	38	35	40

Segments	14	15	16	17	18	19	20	21	22	23	24
Proportions	35	40	35	47	42	40	40	38	45	49	35 = 1000

Exopod of second antenna slightly longer than endopod (Fig. 1D). First protopod segment short, with 1 seta at distomedial margin; second segment twice length of first, with 2 setae at distomedial margin. Exopod 7-segmented; segments 2 and 7 of similar length, segment 1 is half length of these segments, segments 3–6 very short with combined length less than one third length of first segment; first 2 segments devoid of setae, third to sixth each with 1 inner distal seta, seventh with 1 small subapical and 3 terminal setae. Endopod 2-segmented, first segment with 1 medial seta about one quarter length from distal end; second segment with 5 apical setae on lateral lobe, 6 large and 2 minute apical setae on medial lobe.

Mandibular palp with stout basipod bearing 3 inner setae (Fig. 1E). Exopod 3-segmented, first 2 segments each carry a medial distal seta, third segment with 1 medial and 3 apical setae. Endopod as long as exopod, 2-segmented; first segment with medial and distomedial seta, second segment with 9 apical setae. Mandibular blade (gnathobase) only slightly expanded at apex, bears row of 7 sharp denticles (Fig. 1F).

Basipod of first maxilla with 9 lateral marginal setae (Fig. 2A). Medial margin of basipod with 3 processes, large proximal process bears 10 elongate spines, short subterminal process bears 2 setae, long distal process bears 4 setae. Apical lobe of basipod with 5 distal setae. Exopod with 10 setae on distolateral margins. Endopod 3-segmented, first 2 segments each with 3 inner distal setae, terminal segment with 5 setae.

Second maxilla exopod without distinct segmentation (Fig. 2B) but 5 medial lobes are recognisable; first lobe with 5, second and third lobe each with 3 setae, fourth lobe has 1 spine and 2 setae, fifth lobe carries 2 setae and 1 strong inwardly curved pectinate spine. Endopod indistinctly segmented, bearing vermiform aesthetasc distally, 10 brush-like aesthetascs subterminally (Fig. 2C).

Maxilliped 7-segmented (Fig. 2D); first with 4 setae and 2 aesthetascs on medial margin; second with 3 medial setae at midlength and 2 distal setae; third with 3 medial setae; each of segments 4–6 carries 4 setae; terminal segment with 3 setae.

First leg has 2 protopod segments, first without setae, second with distomedial seta (Fig. 2E), both protopod segments with many lines of minute spinules on the surface. Exopod 3-segmented,

distolateral spine on each; first segment has no medial seta, second with 1 medial seta, third with 4 setae around distomedial margin, 2 marginal and 2 apical setae. Only first exopod segment has row of spinules on its surface. Endopod 1-segmented, reaching to distal end of second exopod segment; lateral margin has lobe, apex of which bears numerous spinules; inner margin with 3 marginal setae, 2 apical setae.

Second, third and fourth legs (Fig. 2F–H) are covered with numerous spinules on posterior and anterior surfaces. Those on posterior surface usually larger, those on anterior surface more widespread and consistently near uniform minute-sized. First protopod segment with medial seta, second (basipod) segment devoid of setae on all legs. Spinulation on posterior surfaces of basipod segments rather sparse on second and third legs, but very dense on the fourth. First and second exopod segments with a distomedial seta, lateral marginal spine flanked by 2 minute spines; third segment with 4 medial setae, 2 medial and 1 distomedial spines with serrate margins, 1 large terminal spine with denticulate lateral margin (19 denticles on each). Length of terminal spines slightly greater than that of third segment. Spinules on posterior surfaces of exopods on second and third legs smaller than those on fourth leg. First endopod segment of second leg, first and second endopod segments of third and fourth legs bear medial marginal seta and lateral acute spinous process. Terminal endopod segment with 1 lateral, 2 medial and 2 apical marginal setae on all legs. Spinules on posterior surfaces of endopods are large sized on all legs.

Fifth leg uniramous, symmetrical and 3-segmented (Fig. 2I). First 2 segments of equal length with a few relatively small spinules on medial or distomedial margin. Terminal segment approximately 1.6 times length of penultimate segment, with 1 medial, 1 lateral and 2 terminal spines; medial spine longest, others of similar length; surface of segment covered with numerous (approximately 10) large-sized spines.

Etymology. The species is named in honour of Dr P.C. Rothlisberg of CSIRO Division of Fisheries Research, Cleveland, Australia for providing materials which made this study possible.

Remarks

Brachycalanus is a genus of peculiar benthopelagic copepods which bear close resemblance to *Xanthocalanus* species. The genus was created by Farran (1905) to include *X. atlanticus*, being distinguished from true species of *Xanthocalanus* in the shape of the rostrum and also the short first antenna.

Besides having the characteristics detailed by Campaner (1978) in his redefinition of the genus, *Brachycalanus* can be distinguished from other members of the family by the presence of the knife-

Table 1. Comparison of some characteristics of 5 species of *Brachycalanus*. (Abbreviation used: Th – thorax).

Feature	<i>B. atlanticus</i> <i>sensu stricto</i>	<i>B. atlanticus</i> <i>sensu Farran</i> 1905	<i>B. bjornbergae</i>	<i>B. ordinarius</i>	<i>B. rothlisbergi</i>
Size (mm)	2.5	2.0–2.5	1.6–2.0	2.9–3.4	1.57–1.68
Whether Th4 & Th5 fused/free	fused	free	free	fused	fused
Extent of the 1st antenna length in relation to Th segment	middle end of Th ₁	end of Th ₁	end of Th ₂	middle of Th ₃	middle of fused Th ₄ and Th ₅
No. of denticles on outer margin of terminal spine of legs 2–4	14–15	13	15	10–11	19
Ratio of terminal:penultimate segments of 5th leg	2.4:1	1.64:1	3.0:1	2.83:1	1.67:1
Spinulation of 1st and 2nd segments of 5th leg	dense	dense	dense	dense	sparse

shaped aesthetascs on the 1st antenna. There are eight such aesthetascs which originate from segments 2, 3, 5, 7, 8, 11, 13 and 18 of the first antenna. There are at present four species belonging to this genus. They are *B. atlanticus* (Wolfenden, 1904); *B. ordinarius* (Grice, 1973), *B. bjornbergae* Campaner, 1978, and *B. atlanticus sensu Farran*, 1905. Grice (1973) described *B. ordinarius* as *Xanthocalanus ordinarius* but his species was appropriately transferred to the correct genus by Campaner (1978) (see also Bradford *et al.*, 1983). Two other species have been erroneously ascribed to this genus, *B. gigas* Scott, 1926 was removed to *Lophothrix* (Grice & Hulsemann, 1968, and Bradford, 1973), and *B. minutus* (Grice, 1973) was regarded as *incertae sedis* by Campaner (1978). Bradford *et al.* (1983) listed the genus as having four species but acknowledged the *incertae sedis* status of *B. minutus*.

Farran's (1905) description of *B. atlanticus* differed grossly from *B. atlanticus* (Wolfenden, 1904). The fourth and fifth thoracic segments are fused in *B. atlanticus sensu stricto* but free in *B. atlanticus sensu Farran*; the first antennae, when fully extended, reach the middle of the first thoracic segment in *B. atlanticus s.s.* but reach the end of the second thoracic segment in *B. atlanticus sensu Farran*; the general shape of the fifth legs and their surface spinulations are very different in the two descriptions; also, the shape and length ratios of each of four spines on the terminal segment of the fifth legs are noticeably different in the two descriptions, those being longer in *B. atlanticus s.s.* compared with *B. atlanticus sensu Farran*; and lastly, the ratio of the terminal: penultimate segment of the fifth leg is 2.5:1 in *B. atlanticus s.s.* but is 1.64:1 in *B. atlanticus sensu Farran*. Clearly, then, the two descriptions were not of the same species, Farran's misidentified specimens being of an as yet undescribed species. It is premature for the authors to here name Farran's (1905) specimens.

All species of *Brachycalanus*, including the one described in the present study, are known only from the female.

Brachycalanus rothlisbergi can be distinguished from other members of the genus by the shape and size of the body, the spinulation on the posterior surfaces of legs 1 to 4, the number of denticles on the terminal spines of legs 1 to 4, the shape and spinulation of the fifth leg, and the presence of very prominent and long setae on both lateral surfaces of the third thoracic segment. Detailed differences in body size, shape and relative lengths of the appendages between *B. rothlisbergi* and other members of the genus are given in Table 1.

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Apogon limenus, a new species of cardinalfish (Perciformes: Apogonidae) from New South Wales

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ABSTRACT. *Apogon limenus* is described as a new species from New South Wales. This abundant species has been confused with *Apogon fasciatus*. The species is compared with other striped *Apogon* species which are similar in coloration. It differs from them in details of coloration and the combination of fin ray, scale and gill-raker counts, serrate free margin of the preoperculum and smooth to slightly serrate anterior preopercular ridge.

It is suggested that species collected by HMS *Herald* from "Victoria", were collected from the Victoria District of Western Australia. The district name was used in the 1800's for the area north of Perth and south of Carnarvon.

RANDALL, J.E. & D.F. HOESE, 1988. *Apogon limenus*, a new species of cardinalfish (Perciformes: Apogonidae) from New South Wales. Records of the Australian Museum 40(6):359-364.

The Apogonidae, popularly known as cardinalfishes, is one of the largest families of perciform fishes. Fraser (1972), whose study of the comparative osteology of the group has provided a foundation for the subfamilial, generic and subgeneric classification, estimated that there are 24 to 26 genera and about 200 species in the family. The largest of the genera is *Apogon* which he divided into ten subgenera. The family is in great need of revision in the Indo-west Pacific region at the species level, and as might be expected, the largest number of taxonomic problems lie within the genus *Apogon*, especially in the largest of the subgenera, *Nectamia*.

Many of the Indo-Pacific species of the subgenus *Nectamia* have several dark stripes on the head and body; these are among those most confused by ichthyologists. Fraser (1974) redescribed one of these species, *A. endekataenia* Bleeker, a name often applied to other striped cardinalfishes. Randall & Lachner (1986) differentiated six similar striped species: *A. angustatus* (Smith & Radcliffe), *A. cookii* Macleay, *A. fasciatus* (Shaw), *A. nigrofasciatus* Lachner, *A. novemfasciatus* Cuvier, and *A. taeniophorus* Regan. They also showed that no specimens are known from existing collections that match the description of *A. aroubiensis* Hombron &

Jacquinet, a striped species from Malaysia, the only type specimen of which has been lost.

From the study of Randall & Lachner it became apparent to the senior author (and independently to the junior author) that one of most common fishes of bays and harbours of New South Wales, a large dark-striped species of *Apogon*, is undescribed. This fish has often been misidentified as *A. cookii* (pl. 129 in Grant, 1982) or more commonly as *Apogon fasciatus* White (1790), the type locality of which is Port Jackson (= Sydney Harbour). White named it *Mullus fasciatus* and described it briefly as follows: "Pale yellow Mullet with longitudinal brown bands. Length about five inches; scales large". His illustration of *fasciatus* (reproduced by Radcliffe, 1911, pl. 21), though poor, is unquestionably a species of *Apogon*. There are three dark stripes – one midlateral and two well above it; no dark spot is present on the caudal-fin base. Because of the mention of pale yellow ground color, the lack of two lower stripes, and no indication of a black caudal spot, it seems likely that the Port Jackson fish was the species most ichthyologists have identified as *A. quadrifasciatus* Cuvier. Since there is no type of *fasciatus* extant, Lachner in Schultz & collaborators (1953: 439, pl. 35A) designated USNM 59972, 80.5 mm SL, from

Table 1. Proportional measurements of type specimens of *Apogon limenus* expressed as a percentage of the standard length.

	Holotype		Paratypes					
	AMS	WAM	BPBM	BPBM	BPBM	BPBM	BPBM	BPBM
	I.26325-001	P27082-006	30588	14955	30588	30588	14995	30588
Standard length (mm)	87.3	81.0	85.6	88.0	87.0	93.2	96.2	100.2
Body depth	38.4	48.5	37.4	39.1	38.5	41.0	39.4	38.8
Body width	17.2	18.8	18.1	16.6	16.4	17.1	17.5	17.3
Head length	38.6	40.5	39.7	37.7	38.8	40.7	40.6	39.1
Snout length	9.9	10.0	9.5	9.2	10.1	10.2	9.9	10.0
Orbit diameter	11.7	12.3	11.5	11.1	11.3	11.4	11.6	11.3
Interorbital width	7.8	8.3	7.3	7.6	7.8	8.2	8.3	7.8
Upper jaw length	18.6	18.7	18.4	18.8	18.5	19.2	19.5	19.0
Caudal peduncle depth	17.2	18.2	16.6	17.0	16.5	18.0	16.9	16.1
Caudal peduncle length	23.9	23.5	23.6	23.1	23.8	23.7	23.9	22.7
Predorsal length	41.4	41.2	38.2	39.5	40.1	42.3	42.5	40.5
Prealanal length	60.6	62.4	62.8	60.8	62.0	61.5	60.6	61.5
Prepelvic length	38.4	42.2	43.2	39.2	41.1	39.8	39.1	42.9
Length of first dorsal spine	3.0	3.4	3.6	3.0	3.1	3.2	3.2	broken
Length of second dorsal spine	9.8	9.4	9.5	8.9	9.0	8.8	10.7	aberrant
Length of third dorsal spine	19.5	20.6	19.8	19.6	20.6	21.7	22.5	19.5
Length of spine of second dorsal fin	16.6	15.9	15.8	15.9	17.9	17.0	18.6	17.5
Length of longest dorsal ray	26.4	26.8	28.6	26.4	29.3	27.8	28.7	broken
Length of last dorsal ray	12.0	13.0	13.7	13.3	13.6	12.6	13.5	13.4
Length of first anal spine	3.5	3.1	3.5	3.6	4.2	3.4	3.9	4.1
Length of second anal spine	13.2	13.7	13.6	13.1	15.0	13.9	14.8	14.4
Length of longest anal ray	20.7	broken	23.9	21.6	22.8	21.5	23.0	broken
Length of last anal ray	13.4	14.2	14.5	14.9	15.4	13.8	15.1	15.2
Caudal fin length	28.7	broken	29.3	28.8	30.2	29.2	31.1	broken
Caudal concavity	7.9	—	7.0	7.4	7.1	6.8	7.5	—
Pectoral fin length	24.8	25.9	25.4	24.7	25.2	25.8	26.5	24.9
Pelvic spine length	13.9	14.0	14.6	15.0	15.5	15.2	16.3	15.8
Pelvic fin length	22.0	22.2	22.3	21.8	23.3	22.5	23.8	21.9

Table 2. Gill-raker counts of four dark-striped species of *Apogon* from the Indo-Pacific region. N = specimens from Japan, Taiwan and Hong Kong. S = specimens from New Caledonia, Lord Howe Island and Great Barrier Reef.

	<u>17</u>	<u>18</u>	<u>19</u>	<u>20</u>	<u>21</u>	<u>22</u>	<u>23</u>	<u>24</u>
<i>A. victoriae</i>	17	32	33	3				
<i>A. doederleini</i>								
N		2	10	6	2			
S	2	10	7	3				
<i>A. fasciatus</i>		1	14	10	2		1	
<i>A. limenus</i>				3	11	8	7	1

Port Jackson as the neotype. This is a fish which fits the description of *A. quadrifasciatus* Cuvier; therefore *A. fasciatus* (Shaw) is a senior synonym of *A. quadrifasciatus*. The purpose of the present paper is to provide a description of the common cardinalfish formerly called *A. fasciatus*. Both *Apogon fasciatus* and the new species described here are common in Sydney Harbour.

Methods and Materials

All lengths of specimens are standard length (SL), measured from the median anterior point of the upper lip to the base of the caudal fin (end of hypural plate). Body depth is the maximum depth, and body width the greatest width just posterior to the gill opening. Head length is taken from the front of the upper lip to the posterior end of the opercular

membrane; snout length is measured from the same anterior point to the nearest fleshy edge of the orbit. Orbit diameter is the greatest fleshy diameter. Interorbital width is the least bony width. Caudal peduncle depth is the least depth, and caudal peduncle length is the horizontal distance from the rear base of the anal fin to the caudal-fin base. The lengths of the dorsal and anal spines and rays are measured from the point where they emerge from the scaled part of the body. Caudal-fin and paired-fin lengths are the lengths of the longest rays of these fins (the horizontal distance for the caudal fin; from the base of the initial spine to the tip of the longest ray for the pelvic fin). Caudal concavity is the horizontal distance between the tips of the longest and shortest caudal rays.

The last dorsal and anal rays are a composite of two elements divided from the base; these are



Fig.1. Holotype of *Apogon limenus*, AMS I.26325-001, female, 87.3 mm SL Sydney Harbour, N.S.W.

counted as a single ray. Pectoral-ray counts include the upper rudimentary ray. Lateral-line scale counts are made to the caudal-fin base. Gill-raker counts include all rudiments; the raker at the angle is contained in the lower-limb count.

Specimens of the new species have been deposited at various museums, the abbreviations of which follow Leviton *et al.* (1985).

In the description of the new species, data in parentheses refer to paratypes. Table 1 gives the measurements of selected type specimens as percentages of the standard lengths. Many of these measurements are repeated in the text as quotients of larger measurements such as standard length or head length; these are rounded to the nearest .05. Table 2 provides the total gill-raker counts of the new cardinalfish and those of other larger dark-striped species that occur in eastern Australia with which it might be confused.

Apogon limenus n.sp.

Figs 1, 2

Material examined. HOLOTYPE: AMS I.26325-001, 87.3 mm, female, Australia, NSW, Sydney Harbour, Bottle and Glass Rocks (33°52'S, 151°16'E), rock face with ledges 5–8 m, rotenone, Rudie H. Kuiter *et al.*, 6 Sept 1981. PARATYPES: BPBM 30588, 5: 85.6–100.2 mm, same locality as holotype, J.R. Paxton and class, 6 Aug 1972; BMNH 1986.9.4.129, 93.0 mm, same data as preceding;

BPBM 14955, 2: 88.0–96.2 mm, Australia, NSW, Port Hacking, Little Turriel Point, Ship Rock, 12–15 m, spear, J.E. Randall, 6 Mar 1973; CAS 58973, 94.1 mm, same data as preceding; AMS I.19103-032, 30: 29.8–110.2 mm, NSW, Parsley Bay, Sydney Harbour, rotenone, J.R. Paxton and class, 8 May 1976; AMS I.19700-008, 2: 87.6–88.6, NSW, North Solitary Island, B.C. Russell and J. Bell, 26 Sept 1976; AMS I.19499-001, 94.4 mm, NSW, Vacluse Bay, Sydney Harbour, R.H. Kuiter, 5 Sept 1979; WAM P27082-006, 5: 81.0–96.3 mm, NSW, Solitary Island, W side (30°01'S, 153°16'E), rotenone, J.B. Hutchins, 29 Dec 1980.

Diagnosis. Dorsal rays VII–I,9; anal rays II,8; pectoral rays 14; lateral-line scales 24; gill rakers 5–7 (rarely 5) +14–17; body moderately deep, depth 2.45–2.7 in SL; broad band of villiform teeth in jaws; palatine teeth present; free margin of preopercle serrate, anterior ridge smooth to partially serrate; caudal fin emarginate with rounded lobes; purplish brown with five dark brown stripes on body, midlateral one leading to black spot the size of pupil on basal fourth of caudal fin.

Description. Dorsal rays VII–I,9; anal rays II,8; pectoral rays 14, upper ray rudimentary, second and last rays unbranched; pelvic rays I,5; principal caudal rays 17, upper and lower unbranched; upper and lower procurent caudal rays 7; lateral-line scales 24; scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 2; circumpeduncular scales

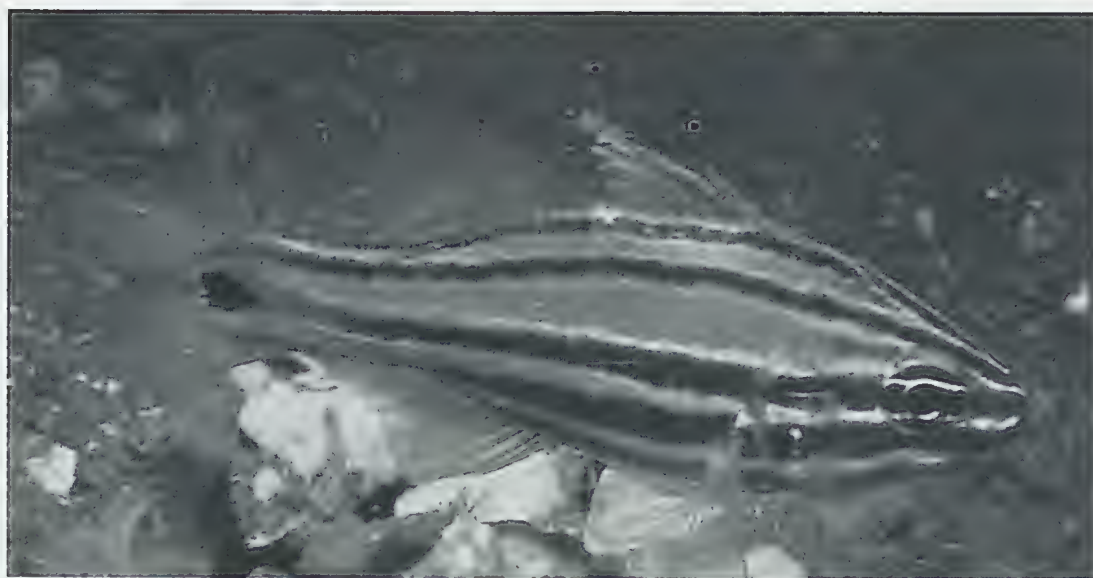


Fig.2. Underwater photo of *Apogon limenus* from Port Hacking, N.S.W., photo J.B. Hutchins.

12; gill rakers 6+16 (5-7+14-17); pseudobranch lamellae 20 (20-24); branchiostegal rays 7; predorsal bones 3; vertebrae 10+14.

Body moderately deep, depth 2.6 (2.45-2.7) in SL, and compressed, width 2.25 (2.05-2.4) in depth. Head length 2.6 (2.45-2.7) in SL; snout length 3.9 (3.85-4.2) in head. Orbit diameter 3.3 (3.3-3.55) in head. Interorbital space flat to slightly convex, the width 4.95 (4.9-5.45) in head. Caudal peduncle depth 2.25 (2.2-2.4) in head; caudal peduncle length notably longer than depth, the depth contained 1.4 (1.3-1.4) times in peduncle length.

Mouth terminal and slightly oblique, maxilla reaching posterior to a vertical through centre of eye, upper jaw length 2.1 (2.05-2.15) in head. Broad band of villiform teeth in jaws, with no enlarged teeth; vomer with rows of small teeth forming a V; palatines with 2 rows of very small teeth, narrowing posteriorly to a single row. Tongue short and pointed, upper surface with 3 converging bands of papillae. Gill rakers moderately long, the longest (at angle) longer than longest gill filaments on first arch, about 2.5 in orbit diameter.

Anterior nostril a small membranous tube in front of centre of eye; posterior nostril a small aperture in diagonal line connecting anterior nostril to top of orbit, nearly half the distance to upper edge of orbit.

Opercle with single, flat, obtuse spine; inner ridge of preopercle smooth or with some irregular weak serrae, particularly at corner and lower edge; free margin of preopercle finely serrate; margins of subopercle and interopercle smooth.

Scales finely ctenoid; head largely naked, only few scales posteriorly on nape, on upper opercle, and in 2 diagonal rows on preopercle (anterior row of 6 scales

and posterior row of 1); no scales on fins except small scales basally on caudal fin.

Dorsal fins well separated, origin of first over base of third lateral-line scale; first dorsal spine small, 6.5 (5.5-7.0) in length of third dorsal spine; third dorsal spine longest, 2.0 (1.8-2.1) in head; longest dorsal soft ray (usually the first) 1.45 (1.3-1.5) in head. Origin of anal fin slightly posterior to origin of second dorsal fin; first anal spine small, 3.8 (3.5-4.2) in second spine; second anal spine 2.9 (2.6-2.95) in head; longest anal soft ray (the first) 1.85 (1.65-1.9) in head. Caudal fin emarginate with rounded lobes, its length 1.35 (1.3-1.4) in head; caudal concavity 4.9 (5.1-5.9) in head. Third or fourth pectoral rays longest, 1.55 (1.5-1.55) in head. Pelvic fins reaching to or beyond origin of anal fin, their length 1.75 (1.65-1.8) in head.

Colour of holotype. Fresh: purplish brown with 5 dark brown stripes; first stripe mid-dorsal on head (beginning in interorbital space), passing along base of dorsal fins, continuing dorsally onto caudal peduncle; second stripe from front of snout, along upper edge of eye, passing just above and parallel to lateral line anteriorly on body, diverging slightly upward from lateral line below second dorsal fin, parallel to dorsal contour of caudal peduncle, and ending on upper base of caudal fin; third stripe about twice as broad as upper two, midlateral from front of snout through eye to a black spot the size of pupil on caudal fin about one fourth distance from base to end of fin and continuing faintly on caudal rays posterior to spot; fourth stripe from front of chin, across mouth, through lower edge of eye, to lower base of caudal fin, this stripe anteriorly on body and postorbital head broader than third stripe, but more

diffuse; fifth stripe from lower chin and posterior maxilla across thorax and abdomen to posterior base of anal fin, this stripe less distinct than others; upper edge of third (midlateral) stripe and space between third and fourth stripes iridescent blue green and yellow; stripes on head yellowish brown, interspaces iridescent blue green and yellow; short yellowish brown stripe on postorbital head between second and third stripes; fins light red, suffused with pale blue, first dorsal with a wash of yellow anteriorly, second dorsal and anal fins with brown band near base; caudal fin with aforementioned centrobasal black spot and terminal ends of 3 median dark stripes (second and fourth stripes yellowish brown within fin).

When viewed underwater live, individuals appear whitish with dark brown or blackish stripes.

Colour in alcohol: light brown, stripes as described above dark brown, midlateral stripe most heavily pigmented; interspaces light brown; basal spot on caudal fin black; peritoneum pale, gut black; intestine black, but lighter than stomach.

Remarks. This species is named *limenus* from the Greek *limen* for harbour or refuge, in reference to its frequent occurrence in harbours and bays.

Apogon limenus is known only from between latitudes 27° and 36°35'S, from Moreton Bay, Queensland to Bermagui, New South Wales. It occurs on rocky bottom at depths of 1 to 20 m. Like other species of the genus it is nocturnally active, remaining in crevices and caves during daylight. Males brood the egg mass in the mouth. It is one of the larger species of *Apogon*; our largest specimen measures 110.2 mm SL.

Apogon limenus might be confused with three other large, dark-striped species of the genus which occur in the sea off eastern Australia: *A. fasciatus* (Shaw), *A. cooki* Macleay, and *A. doederleini* Jordan & Snyder. *Apogon fasciatus* is distinctive in having three dark stripes instead of five, no black spot on the caudal fin base, 15 or 16 (usually 16) pectoral rays (14 for *A. limenus*), and a lower average number of gill rakers (see Table 2). It also differs in its habitat of more open, soft-bottom habitat and is typically taken in trawls. *Apogon cooki* may be differentiated from *A. limenus* by having a dark stripe anteriorly on the body between the second and third stripes (this stripe confined to the head on *A. limenus*), in having 15 pectoral rays, and 20–23 gill rakers (17–20 in *A. limenus*). *Apogon cooki*, although overlapping with *A. limenus* is primarily tropical. *Apogon limenus* is perhaps closest to *A. doederleini*, an antitropical species which occurs in the Northern Hemisphere in Japan, Taiwan, China, and in the Southern Hemisphere on the Great Barrier Reef, Lord Howe Island (the *Apogon* sp. A of Allen *et al.*, 1976), Sydney Harbour, NSW, and New Caledonia [*Apogon angustatus* (non Smith & Radcliffe) of Fourmanoir & Laboute, 1976] and the Kermadec Islands. The latter has five dark brown stripes and a black caudal base

spot, but the stripes are much thinner, and the second stripe follows the lateral line anteriorly on the body (above lateral line on *A. limenus*). The black caudal spot of *A. doederleini* lies on the base of the caudal fin whereas it is centered about one-fourth the way out on the fin in *A. limenus*. In addition, *A. doederleini* has 15 or 16 (usually 15) pectoral rays. The two species sometimes occur together at the same locality and juveniles are particularly difficult to separate, since the bands are often thinner in juveniles of *A. limenus*. Juveniles are separable on the basis of pectoral-ray counts, black caudal spot position, and the dorsal black stripes below the dorsal fins which converge immediately before the first dorsal fin in *A. doederleini*, rather than on the head above the operculum as in *A. limenus*.

Also related is *Apogon victoriae* Günther, which occurs in southwestern Australia. It differs from *A. limenus* in having 5 instead of usually 6 or 7 upper-limb gill rakers and in having broader stripes which are brownish red in life. It also has an extra stripe on the anterior body between the second and third stripes and a black spot on the base and axil of the pectoral fins.

There is some uncertainty regarding the type locality of *Apogon victoriae*. Günther (1859) described the species from a specimen collected by the HMS *Herald* from Victoria. McCulloch (1929) regarded the type locality as the Victoria River in the Northern Territory. However, G. Allen (in litt.) has noted that other species described by Günther (1859) from Victoria are largely tropical and suggested that the type locality might be the Victoria settlement at Port Essington, north of Darwin. If *Apogon victoriae* was described from northern Australia, then *Apogon cooki* would become a synonym of *A. victoriae*. We have been informed by T. Fraser that the dried holotype of *A. victoriae*, although in poor condition, appears to match the Western Australian species, particularly in the black spot at the base of the pectoral fin. In early explorations to Western Australia Grey (1841) named a large area between Perth and Carnarvon as the Province of Victoria. The province is clearly marked on a map produced from early expeditions (Grey, 1841) and this map probably would have been used aboard HMS *Herald*. The clinid, *Heteroclinus antinectes* Günther, was also collected by HMS *Herald* from Western Australia in Freycinet Harbour and is only known from the Shark Bay region of Western Australia; and it is apparent that the *Herald* worked on the Western Australian coast. Consequently, until further evidence becomes available we accept *Apogon victoriae* as the Western Australian species and distinct from the tropical *A. cooki*.

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Bavayia validiclavis and *Bavayia septuiclavis*, two new species of gekkonid lizard from New Caledonia

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ABSTRACT. Two new species of gekkonid lizard, *Bavayia validiclavis* and *Bavayia septuiclavis*, are here described from New Caledonia. Both are small but distinctively coloured, ground sheltering species. *Bavayia validiclavis* occurs on the north-east ranges of the main island, while *B. septuiclavis* occurs in the south of the main island below 22°09'S.

With the addition of the two new taxa described here a total of seven species of *Bavayia* (*B. cyclura*, *B. montana*, *B. crassicolis*, *B. validiclavis*, *B. septuiclavis*, *B. sauvagii*, *B. ornata*) is now known. A key to these species is provided.

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Roux (1913) in a monograph of the New Caledonian reptiles proposed the generic name *Bavayia* for the species *Peripia cyclura* Günther, 1872, and *Lepidodactylus sauvagii* Boulenger, 1883, described several new taxa (*Bavayia cyclura montana*, *Bavayia cyclura crassicolis* and *Bavayia sauvagii ornata*), and identified members of the genus as endemic to New Caledonia and the Loyalty Islands.

I have examined specimens of *Bavayia* in the AM, QM, BM, NHMB, CAS and MNHP, all extant types, and during the course of extensive field work in New Caledonia and the Loyalty Islands have collected all of the species here recognised. In the field most species of *Bavayia* were readily distinguished by certain features of gross morphology (size, colour and pattern) and habit (whether the specimens were collected sheltering under ground debris or bark of trees by day). Subsequent examination of preserved material revealed several scalation characters (see key) which in combination with features of size and colouration allowed most specimens to be readily allocated to those taxa recognised by Roux (1913) (which I here treat as distinct species); however two taxa could not be allocated to any named species. In this paper I describe these species and diagnose the currently recognised taxa via a phenetic key.

Materials and Methods

Specimens of *Bavayia* were examined from the collections in the Australian Museum Sydney (AM), Queensland Museum (QM), Naturhistorisches Museum Basel (NHMB), British Museum of Natural History (BM), Museum National d'Histoire Naturelle Paris (MNHP), and California Academy of Sciences (CAS).

Measurements and scalation were assessed from whole alcoholic specimens. These features of morphology and the corresponding abbreviations are defined as follows.

Measurements: snout to vent length (SVL), distance from snout to margin of vent; tail length (TL), distance from tail tip to margin of vent; head length (HDL), distance from anterior margin of external ear opening to tip of snout; head width (HDW), distance across head at subocular upper labials; snout length (SNL), distance from anterior margin of eye to tip of snout.

Scalation (follows Kluge 1965): supralabials, scales bordering lip margin of upper jaw posterior of rostral to below centre of eye; rostral, enlarged scale at tip of snout; supranasal, enlarged scale bordering nostril and contacting rostral anteriorly; postnasal, scales bordering nostril and contacting supranasal

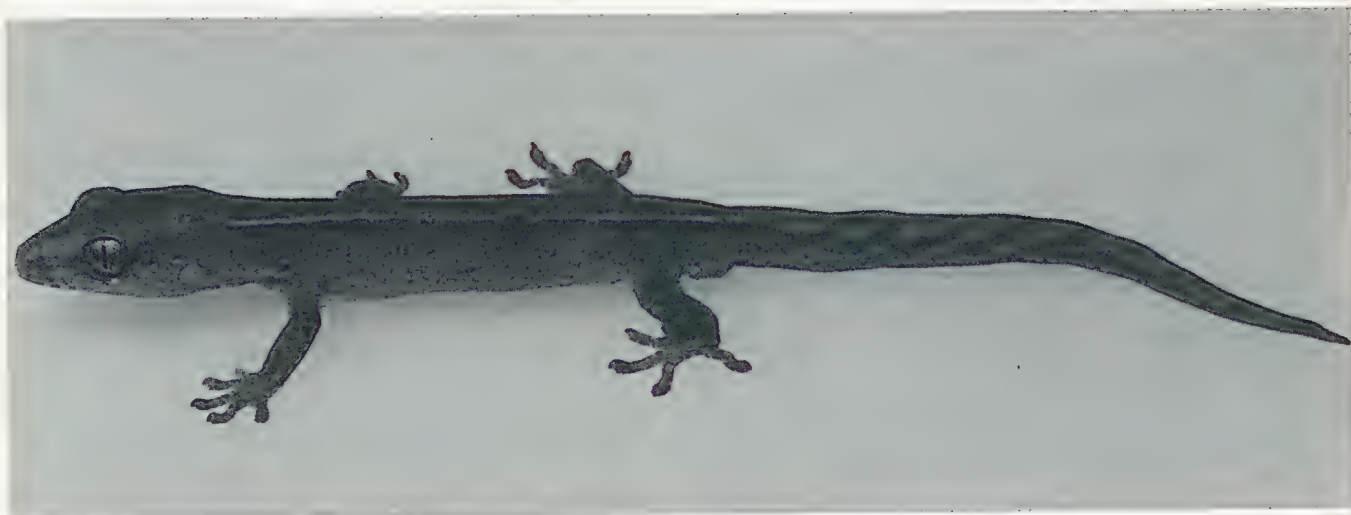


Fig.1. *Bavayia validiclavis* from Mount Panie (500m), New Caledonia.



Fig.2. Holotype of *Bavayia validiclavis* AM R77855.



Fig.3. Holotype of *Bavayia septuiclavis* AM R78139.

anteriorly; internasal, scale bordering rostral and contacting supranasals laterally; first infralabial, scales either side of mental and bordering margin of lower jaw; preanal pores, external openings of preanal glands located within scales anterior to vent; cloacal spurs, enlarged projecting scales at lateroventral margin posterior to vent; lamellae, scales covering the underside of fourth digit from apical plate to margin separating third and fourth digits.

***Bavayia validiclavis* n.sp.**

Figs 1, 2, 4

Type material. HOLOTYPE: AM R77855 an adult male (Fig. 2) from Mount Panie (500–600 m), 20°33'S, 164°45'E, New Caledonia. Collected by R.A. Sadlier and P.R. Rankin, 17 Dec 1978. PARATYPES: QM J43980 Mandjelia near Pouebo, 20°23'S, 164°33'E; AM R77847, R77853–54, R77856–58, R77895, R77353, same locality as holotype; MNHP 1980-1067 Mount Panie.

Diagnosis. A small species of *Bavayia* (maximum SVL 45 mm) distinguished from its congeners by the following combination of features of scalation and colouration: claw of inner toe asymmetrically positioned within a groove in the apical lamella shield; 2 rows of preanal pores, 12–16 on anterior row; first pair of infralabials moderately to widely separated; supranasals separated by a large single internasal scale; dorsal colour pattern featuring a distinct, broad, pale vertebral stripe rather than variably defined dark, transverse bars.

Description. This description is based on 4 adult males (SVL 42–44 mm), 4 adult females (SVL 41–45 mm), and 1 subadult (37 mm). Only adults are included in the measurements.

Measurements: HDL 22.7–25.2% of SVL (\bar{x} = 23.5, n = 8); HDW 13.9–16.4% of SVL (\bar{x} = 15.1, n = 8); SNL 38.1–45% of HDL (\bar{x} = 42.9, n = 8); TL 109.3% of SVL (n = 1).

Scalation: supralabials 7–8 (66.6%, n = 9); nostrils each surrounded by rostral, supranasal, 1–2 (66.6%, n = 9) large upper postnasals, 1–2 (55.5%, n = 9) smaller lower postnasals, first supralabial scales; supranasals separated by large single internasal divided unevenly to form 2 scales in QM J43980; first pair of infralabials moderately to widely separated from contacting medially; preanal pores 12–16 (\bar{x} = 14.7, sd = 1.6, n = 4) on anterior row (continuity of AM R77853 broken at apex by single scale lacking a pore), 8–11 (\bar{x} = 9.7, sd = 1.1, n = 4) on posterior row; cloacal spurs 1–3, usually 2 (50%, n = 4); fourth toe lamellae 10–12 (\bar{x} = 11.1, sd = 0.6, n = 9), variably divided over length of digit.

Colouration: usually mid brown with light brown-tan vertebral stripe, defined on either side by a narrow pale stripe (paler than vertebral stripe) innermost and an adjacent narrow dark stripe (darker than general body colour) outermost. Light and dark edging to pale vertebral stripe most obvious

in region of fore limb but tending to fade posteriorly. Otherwise body colour mid grey (QM J43980, NHMP 1980-1067) or darker brown (AM R77857, R77895) with broad, pale vertebral stripe variably defined but always discernable. Supralabials each with a white blotch on posterior edge of each scale, infralabials, chinshields and throat with fine brown spotting, remainder of ventral surface with or without fine dark spotting. Tail with pale blotches (same colour as vertebral stripe) dark edged posteriorly.

Details of holotype: HDL 10.5 mm; HDW 6 mm; SNL 4 mm; supralabials 6/6; supranasal 1, postnasals 4 (2 uppermost large, 2 lowermost small); supranasals separated by large, single internasal; first pair of infralabials moderately separated from contacting medially. SVL 43 mm; preanal pores 16 on anterior row, 10 on posterior row; TL 47 mm, original; cloacal spurs 1/1; fourth toe lamellae 12/12 from distal tip to base of webbing between third and fourth toe, anteriormost undivided, following 3–4 with a median groove, remainder except most basal undivided.

Distribution and habits. *Bavayia validiclavis* occurs in the northeast ranges of the main island of New Caledonia. It is sympatric with both *B. montana* and *B. ornata* in closed forest habitat on the mid to lower slopes of Mount Panie in the north-east of the main island. Individuals were collected by day beneath rocks and logs on the forest floor. The area was not surveyed at night.

Etymology. The name is derived from the Latin *validus* (= strong) and *clavis* (= line or bar) and alludes to the distinctive vertebral stripe on the dorsal surface of this species.

***Bavayia septuiclavis* n.sp.**

Figs 3, 4

Type material. HOLOTYPE: AM R78139 an adult male from 4 km along Mount Gouemba road from turnoff on Yate-Goro road (300–350 m), 22°09'S, 166°54'E, New Caledonia. Collected by R.A. Sadlier and P.R. Rankin, 27 Dec 1978. PARATYPES: QM J44034, J44985, AM R125291-93 Riviere Bleu Forest Reserve, ca. 22°06'S, 166°40'E; AM R78140-41; R90193, same locality as holotype; AM R78339, R125888 Mount Koghi, 22°10'S, 166°32'E; AM R78234-36, 2 km north-east of Pic du Pin, Plaine de Lacs, 22°15'S, 166°50'E; MNHP 1985-120 and 1985-121, Vallee de la Coulee, 22°11'S, 166°36'E.

Diagnosis. A small species of *Bavayia* (maximum SVL 50 mm) distinguished from its congeners by the following combination of features of scalation and colouration: claw of inner toe asymmetrically positioned within a groove in the apical lamella shield; a single row of 8–14 preanal pores, often interrupted; first pair of infralabials usually narrowly to moderately separated; internasal region fragmented, usually with 3–5 small scales bordering the rostral; dorsal colour pattern featuring a broad



Fig.4. Distribution of *Bavayia validiclavis* (closed circle) and *Bavayia septuiclavis* (closed star).

but variably defined light vertebral stripe rather than dark transverse bars.

Description. This description is based on 5 adult males (SVL 45–49 mm), 6 adult females (SVL 44–50 mm) and 4 subadults (3 males SVL 36–42 mm and 1 female SVL 35 mm). Only adults are included in the measurements.

Measurements: HDL 22.4–25.4% of SVL (\bar{x} = 24.8, n = 11); HDW 14.4–17.8% of SVL (\bar{x} = 15.8, n = 11); SNL 40–43.8% of HDL (\bar{x} = 42.4, n = 11); TL 110.2% of SVL (n = 1).

Scalation: supralabials 7 (46.6%, n = 15), 8 (46.6%) or 9; nostrils each surrounded by rostral, supranasal, 2 (84.7, n = 15) – 3 large upper postnasals and 1 (26.7%, n = 15), 2 (66.7%) or 3 small lower postnasals, and first supralabial scales; supranasals separated by 1–5, usually 3 (66.7%, n = 15) scales in

the internasal region bordering the rostral; first pair of infralabials usually moderately to narrowly separated (80%, n = 15), rarely narrowly contacting; single row of 8–14 (\bar{x} = 10.4, sd = 1.8, n = 8) preanal pores, often interrupted by presence of 1–3 non-pore bearing scales medially, or towards end (MNHP 1985–120) of pore row; cloacal spurs 2 (62.5%, n = 8) – 3; fourth toe lamellae 11–12 (\bar{x} = 11.3, sd = 0.5, n = 15), variably divided over length of digit.

Colouration: light-mid brown or grey usually with an obscure lighter vertebral stripe (rarely obvious, as in MNHP 1985–120), variably defined anteriorly by faint, narrow, pale and/or dark markings either side. Most individuals with some pale (as light or lighter than vertebral stripe) spotting to the body outside of the vertebral stripe. Supralabials, infralabials, chinshields and throat variably pale or dark, usually

corresponding to the body colour, remainder of ventral surface pale.

Details of holotype: HDL 11.8 mm; HDW 7.5 mm; SNL 5 mm; supralabials 7/7; supranasal 1, postnasals 3 (2 uppermost large, lowermost smaller); supranasals separated by 3 small scales in the internasal region bordering the rostral; first pair of infralabials moderately separated medially; SVL 47 mm; preanal pores 8, row discontinuous, 4 pore bearing scales either side of a single non-pore bearing scale; TL 42 mm, reproduced; cloacal spurs 2/2; fourth toe lamellae 11/12 from distal tip to base, of webbing between third and fourth toe anteriormost undivided, remainder with a strong (distally) to weak (basally) median groove.

Distribution and habits. *Bavayia septuiclavis* occurs in the south of the main island of New Caledonia. *Bavayia septuiclavis* was sympatric with *B. sauvagii* at 2 localities. In mid-altitude closed forest habitat at Mount Gouemba both *B. septuiclavis* and *B. sauvagii* were active at night on trunks and branches of roadside trees, 0.5–2 metres above ground level. At Mount Koghis *B. septuiclavis*, *B. sauvagii* and *B. crassicolis* were active at night on the trunks and branches of trees bordering a clearing in mid-altitude closed forest habitat, and *B. septuiclavis* and *B. sauvagii* were collected sheltering by day beneath stones at the edge of the forest clearing.

Etymology. The name is derived from the Latin *septuosus* (= obscure) and *clavis* (= line or bar) and alludes to the obscure vertebral stripe on the dorsal surface of this species.

Comparison with Other Species

Morphology. In general body form and external appearance *B. validiclavis* and *B. septuiclavis* are most similar to one another. The broad, pale, vertebral stripe on the dorsal surface of *B. validiclavis* (distinct) and *B. septuiclavis* (discernable - obscure) will distinguish both these taxa from other species of *Bavayia*; all of which have dorsal colour patterns featuring pale, dark edged transverse blotches. *Bavayia validiclavis* and *B. septuiclavis* differ in the condition of the preanal pores (a double vs single row), the internasal region (supranasals separated by a single large scale vs supranasals separated by several small scales bordering the rostral), and in colouration by definition of the light vertebral stripe (see above).

The claw of the inner toe of *Bavayia* species is positioned either at the inner edge of an undivided apical lamella shield (*B. sauvagii*, *B. ornata*), or within an asymmetrically positioned groove at the distal edge of the apical lamella shield (*B. cyclura*, *B. crassicolis*, *B. montana*, *B. validiclavis*, *B. septuiclavis*). In the latter case the groove in which the claw is located is positioned off centre towards the inner edge of the toe. The positioning of the claw

of the inner toe within a groove in the apical lamella shield will serve to distinguish *B. validiclavis* and *B. septuiclavis* from both *B. sauvagii* and *B. ornata*. *Bavayia validiclavis* may be further distinguished from *B. sauvagii* and *B. ornata* in having a double vs a single row of preanal pores.

Bavayia validiclavis and *B. septuiclavis* share the positioning of the claw of the inner toe (above) with *B. cyclura*, *B. crassicolis* and *B. montana*. Aside from colouration (see above) both *B. validiclavis* and *B. septuiclavis* can be further distinguished from *B. cyclura*, *B. crassicolis* and *B. montana* in having fewer, 10–12 vs 12–16, subdigital lamellae. *Bavayia septuiclavis* can be further distinguished from these taxa in having a single vs a double row of preanal pores.

Distribution. *Bavayia validiclavis* and *B. septuiclavis* are allopatrically distributed. *Bavayia validiclavis* occurs in the northern part of the island ca. 200–250 km distant from the nearest recorded *B. septuiclavis*. *Bavayia septuiclavis* is restricted to but widespread over the southern part of island, a pattern of distribution shared with the gekkonid lizard species *Rhacodactylus auriculatus* and *Rhacodactylus sarasinorum*, and the scincid lizards *Graciliscincus shonae*, *Tropidoscincus rohssii*, *Sigaloseps deplanchei* and *Nannoscincus mariei* (Sadlier 1986). The apparent absence of *B. validiclavis* or *B. septuiclavis* from the central part of the main island is unlikely to be an artifact of collection. In this region substantial collections have been made on the east coast in the vicinity of Canala (21°32'S) by Roux and Sarasin, and in the central highlands (500 m above sea level) at Mount Aoupinie (ca. 21°08'S) by Sadlier and Rankin. Based on my examination of these collections no specimens of either of the new species described here have been collected.

Bavayia validiclavis and *B. septuiclavis* have each been recorded sympatric with 1–2 other *Bavayia* species. The general distribution pattern of *Bavayia* over the main island is that at most localities a member of each inner toe type occur in sympatry, and that the species with the condition in which the claw is positioned within a groove in the apical lamella shield shelters by day in aboreal refuges and the species with the claw positioned on the inner edge of an undivided apical lamella shield shelters by day in terrestrial refuges. *Bavayia validiclavis* and *B. septuiclavis* are anomalous in not sharing the aboreal sheltering habits of the species with which they share inner toe morphology, but rather occupy similar habitats, and in some cases occur in microsympatry with those species having different inner toe morphology.

Key to the Genus *Bavayia*

1. Claw of inner digit of manus and pes positioned within a groove in the apical lamella scale, the outer part of which is larger 2
 —Claw of inner digit of manus and pes positioned on inner edge of the undivided apical lamella scale 6
2. Moderately small species with maximum SVL 50 mm; colour pattern of dorsal surface longitudinally orientated, featuring a broad, light vertebral stripe 3
 —Moderate to large sized species with maximum SVL greater than 60 mm; colour pattern of dorsal surface transversely aligned, featuring a series of large, variably defined, pale blotches each edged with a dark bar posteriorly 4
3. Preanal pores in 2 distinct rows; supranasals usually separated by a single internasal scale; from northeast ranges of main island *Bavayia validiclavis*
 —Preanal pores in a single row; internasal region fragmented, usually with 3–5 scales bordering rostral; from south of 22°09'S on main island *Bavayia septuiclavis*
4. Preanal pores (males only) usually 20 or more on anterior row; first pair of infralabials usually in moderate to broad contact medially; from central and northern highlands of main island *Bavayia montana*
 —Preanal pores (males only) usually less than 20 on anterior row; first pair of infralabials usually narrowly to moderately separated 5
5. Moderate sized species with maximum SVL 63 mm; nape variably with obscure to distinct, pale laterodorsal bars tending to converge medially towards forelimbs, dorsal surface of body posterior to forelimbs variably with obscure to distinct dark transverse edging to pale blotches; from north-east and south-west lowlands of main island, and Ouvea, Lifou and Mare Islands of the Loyalty Islands group *Bavayia cyclura*
 —Large species with maximum SVL 80 mm; nape usually with indistinct pale laterodorsal bars, dorsal surface of body posterior to forelimbs with obscure dark edging to poorly defined pale blotches; from south-east lowlands of main island, and Lifou and Mare Islands of Loyalty Islands group *Bavayia crassicollis*
6. Cloacal spurs (males only) rounded, blunt at tips; lateral surface and hindlimbs brown with numerous pale spots contrasting boldly with dark body colour; from north-east ranges of main island *Bavayia ornata*
 —Cloacal spurs (males only) wedge-shaped, pointed at tips; lateral surface and hindlimbs without distinct pattern of pale spots, at best a few pale spots or blotches variably distinct from darker base colour; from north-east and southern lowlands of main island, and Mare Island of Loyalty Islands group *Bavayia sauvagii*

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